SEXUAL DIMORPHISM IN PRIMATES

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by

LESLEY ANITA WILLNER

Department of Anthropology,
University College London,
Gower street,
London, WC1E 6BT.

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It is taken for granted in human societies that men are, on average, slightly taller, larger and heavier than women, despite a considerable overlap in their respective weight distributions. However, among mammals in general, intersexual size differences within a single species do not always favour males and range from leopard seals, with the female 20% longer and correspondingly heavier than the conspecific male, to gorillas with the male almost twice the size of his mate.

There is ample evidence that body size plays a fundamental role in relation to an animal's survival. Consequently, when males and females of the same species attain different adult body weights, these should be seen in the overall context of divergent life history strategies, as emphasised by the typically later achievement of sexual maturity in the larger bodied sex.

Most explanations of sexual size dimorphism in primates tend to be male-centred. They typically emphasize competition between males for females and protection of the social group by larger bodied males. However, such accounts are commonly marred by circular arguments and post hoc rationalisations. They are also self-defeating in their neglect of the possible effects of natural selection acting on females. The present research examines the ontogeny of sexual size dimorphism in terms of the divergent energetic needs of males and females.

An allometric approach has been adopted, and the frustrations of circularity overcome by exploiting the special relation which exists between brain size and body weight. The results indicate that, at least for simian primates, body size reduction in females has played a major role in the evolution of sexual size dimorphism. For several species of larger bodied primates this difference has apparently been enhanced by body size increase in males. The scaling of molar tooth area with body weight corroborates these findings.

CONTENTS

Continued.....

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

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CHAPTER 1

INTRODUCTION

1.1 OVERVIEW

The advent of sexual reproduction has clearly had profound implications for evolutionary history. It has also led to the somewhat extraordinary phenomenon of sexual dimorphism. It seems quite remarkable that animals which inhabit the same physical environment and share an identical phylogenetic background should be unlike in so many respects. Males and females tend to differ most obviously in relation to overall adult body size, ornamentation and general colour. However, these are only the immediately visible aspects that distinguish between the sexes. There are other, more subtle distinctions ranging from differences in the relations between individual bodily dimensions and divergent dental morphologies to dissimilar behavioural repertoires. These differences are prevalent in a wide variety of species drawn from such disparate classes of animals as fish, birds and mammals. Yet the many examples of both mild and extreme sexual dimorphism are matched by observations of monomorphic species, such as the dusky titi, Callicebus moloch, in which the sexes appear to be alike in every detail (Kinzey, 1972), apart from those features involved

in primary sexual function. The range of variation in both the mode and intensity of sexual dimorphism has led to several suggested explanations but, whilst each of these is appropriate in some situations, none would seem to be universally applicable. The present research seeks to clarify the issue.

The prevalence of sexual dimorphism testifies to the biological importance of secondary sexual differences. At the same time, there is considerable variety in the expression of sexual dimorphism, even within a family. Thus, among Old World monkeys, males are often considerably larger than females and may have longer hair on the crown (e.g., barbary ape, Macaca sylvanus) or longer tails (e.g., white-cheeked mangabey, Cercocebus albigena). Baboon males may be almost twice the size of females and mature males of several species have heavy manes which are lacking in younger males and females (e.g., olive and hamadryas baboons). The degree of size dimorphism is very varied among guenons. Male vervets are about 40% larger than females, whilst patas males are roughly double the size of females. Both sexes of vervets and most other guenons look very similar in other respects and the striking black and white coloration of the diana monkey, with its distinctive patches of chestnut on its back and hind limbs, is common to both males and females.

In contrast, the lower part of the limbs of male patas monkeys are pure white whereas those of the much smaller females are fawn or yellowish white. Male and female hylobatids are approximately the same size, but whilst both sexes of siamang are entirely black, male and female gibbons often differ in colour. Male gibbons of the species Hylobates pileatus are completely black whereas the females are buff coloured with only a black cap. Hoolock gibbons are born greyish-white and darken to black at a few months old. It is particularly interesting that the female's colour then fades, at puberty, so that she is a yellow-brown when adult in contrast to the blackish- brown male. This remarkable diversity calls for some explanation. Unfortunately, owing to the large numbers of variables involved, it is relatively easy to find reasons to account for specific cases of sexual dimorphism and correspondingly difficult to develop a more general framework. This is probably due, at least in part, to the immense complexity of life that followed in the wake of propagation by sexual reproduction.

The evolutionary path from basic organisms that multiply by simple fission to sexually reproducing mammal species is long. Even when twinning occurs, unless through the splitting of a single fertilised ovum, the resulting offspring will not be identical to each other, in the

manner of simple clones, nor will they be exact replicas of their parents. In general, those variations which benefit an individual in relation to its environment will also tend to increase its reproductive success. It is likely to live longer and to compete more effectively than other, less well adapted animals. Sexual reproduction promotes the spread of favourable traits through a population by means of both intrasexual and intersexual selection (see 1.2.1 and 1.2.2). It also permits the gene pool of a species to be carried at split risk with female mammals emerging as the more conservative sex and males showing greater diversity at the expense of carrying a higher risk. However, the loss of a proportion of its males may indirectly lead to an improvement in the overall quality of a population. There would seem to be no restriction on the number of females that can be mated by the fittest and most successful males (Trivers, 1972). The additional offspring fathered by these animals could then replace the lost potential of the supplanted, and therefore presumably inferior, males. It is quite conceivable that the new generation would benefit from a high quality paternal inheritance and that this could be advantageous.

However, populations are made up of individuals and, whereas both sexes seek to mate and produce viable

offspring, the strategies and attributes that promote personal survival and successful reproduction are likely to differ between males and females. Selection may then favour intersexual differences in both behaviour and morphology. Moreover, the abundance of extant sexually dimorphic mammal species suggests that there should be some unifying thread, some common cause that merely differs in its mode of expression according to the varying sets of environmental constraints.

The present enquiry has been confined to an examination of differential body size. This was partly in the interests of comparability between species, since this aspect is probably the most comprehensive readily quantifiable form of sexual dimorphism. However, there was also a more compelling reason for the choice. This lay in the many indications that an animal's overall body size has far reaching implications for its survival.

1.2 SIZE AND SURVIVAL

Schmidt-Nielsen (1972) convincingly demonstrated that "The size of an animal is one of the most significant aspects of its endowment and involves both possibilities and limitations in regard to function". Moreover, examples abound which indicate that body weight is likely to be very tightly constrained during periods of stress. It may

even be a major factor in determining survival under critical conditions when successful competition with other individuals becomes a crucial imperative. This is presumably true throughout each developmental stage and focuses attention on the ontogeny of sexual size dimorphism as a potential source of insight into the nature and adaptive significance of intersexual differences between adults. Indeed, both Clutton-Brock et al. (1985) and Lee (1985) have shown that fast-growing males may be subject to higher mortality than females during ontogeny. This introduces the problem of differential survival of males and females in utero, perinatally and during the first year of life. It is especially important to seek an explanation for variations in mortality between the sexes at this early age since sexual dimorphism in body size is typically absent at birth, during infancy and between juveniles and in most cases only becomes noticeable just prior to sexual maturity. The immediate post-natal period is notably a time of peak mortality and maximum vulnerability to predation for both sexes and young juveniles remain at high risk. Passerine mortality is such that nearly 50% of 1-year old birds are dead a year later (Taylor, 1985). As a striking example among mammals, the survival rate among cheetah cubs is only about 1 in 10 (Eaton, 1974) and of the infants born into a troop of yellow baboons in

Amboseli National Park, Kenya, not more than one third survived the 22 months until the birth of their mother's next infant (Altmann et al., 1977). It may be significant that male and female body weights appear to coincide most closely at precisely these ages, even among those mammal species which subsequently exhibit a high degree of sexual dimorphism in adult body size. Now there may be a maternally orientated explanation for this apparent conservatism in the initiation of intersexual differences in body size, or it may be that lack of energetic resources inhibits too rapid early growth. However, whichever alternative seems more plausible in accounting for the conspicuous absence of sexual size dimorphism at this early age, there is no shortage of precedents linking survival with a particular body size, whether or not the divergence occurs along sexual lines.

Stein (1950), in a study of the European mole, Talpa europea, showed that only small individuals were favoured by the sub-optimal conditions at high altitude which reduced food availability due to prey migration in winter and dessication during the summer. Amadon (1959) observed that in highly dimorphic species of birds, larger males were more vulnerable than females both to certain predators and to climatic extremes. Johnston et al. (1972), in a reappraisal of data first presented by Bumpus

in 1899, noted that for house sparrows, Passer domesticus, both body weight and wing span appeared to be of differential benefit to males and females. A marked contrast was found in the degree of sexual size dimorphism present in samples of survivors and non-survivors of a severe storm. Discriminant scores based on six skeletal characters failed to separate the non-survivors adequately into male and female classes, whereas survivors of the same storm were classified according to sex with only a small percentage error; the multivariate difference between the means for survivor sex classes was also highly significant. These findings suggest that relatively small percentage size differences (e.g. 1.1% in humerus length and 3.7% in sternal length) may be highly significant in terms of survival and that under extreme stress each sex of a given organism may favour a different optimum located within very narrow and precisely defined limits. Directional selection was also noted in a small population of Darwin's medium ground finches, Geospiza fortis, under conditions of climatic adversity (Price et al., 1984). Large beak and body size were favoured in 1977, a time of diminishing food supply and high adult mortality. In two subsequent periods of moderate to high adult mortality (1980 and 1982), the population was again subject to the same selection. However, it seems that the strong potential for microevolutionary change in adult

body weight between generations is only realised to a very limited extent. Selection for an overall increase in body weight must take account of the viability of the individual at each intervening stage in the life cycle. Price and his colleagues ascribed the small net effect to opposing selection pressures at an earlier developmental stage, most notably in association with juvenile mortality. Small individuals seemed to have a selective advantage over large individuals in their first two to ten months. Although there was no comment regarding the influence of hatching weight on either immediate survival or subsequent mortality, these results appear to be somewhat at variance with the correlation between survival and birth weight among human infants (Frisch, 1977). The discrepancy is probably most instructive in highlighting the dangers inherent in assuming continuity of effect between widely different types of organism.

1.3 ECOLOGICAL IMPLICATIONS OF BODY SIZE

In general, animals utilise their habitats very differently according to their size. Metabolic rate scales to the power 0.75 (Kleiber, 1961), so that small animals must gain access to high quality, energy rich foods, such as ripe fruit and insects, whereas larger individuals, with a slower metabolic rate, can subsist on nutritionally inferior items which they consume in greater quantity.

This change in diet appears to be dictated by food availability rather than choice. The decrease in metabolic rate that typically accompanies an increase in body weight means that larger animals require less food per unit body mass than smaller animals. Nevertheless, they still need more in absolute terms. Thus, the spatial distribution of a group is heavily influenced by the size of its individual members; for instance, a field that can support five hundred mice can only sustain two horses (Peters, 1983). In general, an increase in overall body size brings in its wake a whole mosaic of inter-related effects. For example, bigger animals sleep less and benefit from energetically cheaper locomotion than smaller animals (Schmidt-Nielsen, 1984). Yet, although they can range further, they may still be unable to satisfy their increased total food needs entirely from high energy items. Harvey et al. (1987) have cited evidence that "the absolute quantity of insect food obtainable increases only marginally with increasing body size of the primate predator, such that larger-bodied primates are obliged to eat a greater proportion of plant food". At the same time, they are denied access to the young leaves and fruit at the ends of terminal twigs that cannot bear the weight of larger, heavier animals. These individuals must resort to the older, coarser leaves that would be indigestible to smaller animals. Nevertheless, there is a dietary penalty;

although foliage is more evenly and densely distributed than other foods, much of its nutritional value is locked in the structural material of the cell walls (Dunbar, 1988). Folivores must either accept a lower rate of nutrient extraction and become 'bulk' feeders (e.g., gelada: Dunbar, 1984; gorilla: Fossey and Harcourt, 1977, Goodall, 1977) or develop specialised digestive strategies (e.g., colobines: Kay et al., 1976; howler monkeys: Milton and McBee, 1982). Dunbar (1988) has suggested that these specialised structures might "both be expensive to evolve and impose major limitations on the animals' options in other respects". The enforced switch from an energy-rich diet to poorer quality food may well limit the response to selection for further increase in overall body size.

In order to survive, an animal must find sufficient food to balance its energy budget without being caught by a predator in the process (Dunbar, 1988). Predator avoidance tactics are clearly size dependent. Whereas a cryptic strategy may be highly effective for the tiny, secretive loris, it would scarcely be viable for a large and conspicuous animal. Bigger species adopt a variety of alternative predator avoidance strategies, some favouring speed of escape (e.g., impala), others developing formidable weapons, such as the large canines of baboons.

There is an old cliche "the bigger you are the more likely you are to eat and the less likely to be eaten". On the other hand, although bigger animals have fewer predators, these are also less likely to be preyed upon, so that an ecological balance will still ensue (Peters, 1983). Such considerations have implications for the social organisation and life history strategy most suited to a species. Whilst a detailed examination of these issues is outside the scope of the present study, they are nevertheless recognised as essential concomitants of body size.

Most importantly, it is features like metabolic scaling that lie at the heart of body size scaling of other variables. Moreover, in addition to basic physiological differences between the sexes, females must be able to sustain a heightened metabolic turnover during reproduction.This is likely to be a critical factor in determining the body size at which a female can successfully reproduce and may well be a key element promoting intersexual size differences between mature males and females.

1.4 THEORIES OF SEXUAL SIZE DIMORPHISM

Even when the study of sexual dimorphism has been restricted to the consideration of those factors which

might promote intersexual differences in body size, there remains an embarrassing diversity in the range of proposed explanations. The nature of these accounts serves to highlight the problem of setting sexual size dimorphism in an evolutionary context. In particular, many are flawed by their unacknowledged failure to differentiate between primary causes and secondary consequences as well as by their lack of consistency with certain known facts. Nevertheless, they still merit serious consideration since they have enjoyed such wide currency. The most frequently suggested theories have been summarised by Harvey and Bennett (1985). They listed six major hypotheses which attempt to account for the observed variation:

1) Intrasexual selection

2) Intersexual (or epigamic) selection

3) Post-mating sexual selection

4) Niche expansion

5) Anti-predator defence

6) Divergent energy strategies

Each of these theories is now discussed.

1.4.1 Intrasexual selection

One of the most popular male-orientated explanations has always been that bigger males can more effectively

compete with one another for females (see Alexander et al., 1974; Clutton-Brock et al., 1980; Crook and Gartlan, 1966; Darwin, 1871; Goss-Custard et al., 1972; MacKinnon, 1977; Struhsaker, 1969; Trivers, 1972; Wilson, 1975). However, size may not always be paramount in determining dominance ranking. Ralls (1976) has cited examples indicating that the "importance of relative body size in determining the outcome of agonistic encounters varies widely in mammals" and that rank is not always correlated with weight (see also Meese and Ewbank, 1973; Fleming, 1974). The hornless female dik-dik is larger than the apparently more aggressive, horned male and there are other species for which the female is the larger sex, although the male is probably the more aggressive (African water chevrotain: Dubost, 1975; cheetah: Kingdon, 1977; dik-diks and duikers: Hendrichs and Hendrichs, 1971; Ralls, 1975; Weddell seal: Smith, 1966). Nevertheless, for many species, male fighting prowess is likely to be linked to body size.

1.4.2. Intersexual (or epigamic) selection

The outcomes of intersexual and intrasexual selection are unlikely to be entirely independent. A female with the opportunity to choose may be selected to seek a mate with those heritable attributes that would benefit their joint offspring. This would lead her to prefer a male with those

characteristics favoured by intrasexual selection (Fisher, 1930, Harvey and Bennett, 1985; Trivers, 1972). The consequences of intersexual selection are frequently expressed as dimorphism in fighting weapons which 'impress' the opposite sex. Females are also apparently 'charmed' by more bizarre attributes, such as the ornamental tail of the peacock or the long tail of the African widow bird, neither of which yields any advantage in inter-male combat (Andersson, 1982). Perhaps these features are attractive because they render the male more conspicuous and possibly reduce the risk of predation for the female and offspring.

1.4.3. Post-mating sexual selection

Post-mating selection has probably made no impact on overall adult body size dimorphism. Its influence, which has most likely been enhanced by intersexual selection pressures, would rather have tended towards the evolution of increased testes size and female sexual swellings, given the appropriate setting (Harvey and Bennett, 1985). During oestrus, female gorillas mate with only one male (Harcourt, 1981) whereas chimpanzee females are promiscuous to the extent that more than 25% of conceptions reportedly followed matings with more than one male (Tutin, 1980). This would tend to place a premium on sperm production. In general, larger species need larger

testes to offset the dilution which occurs in the correspondingly larger female reproductive tract, since sperm production per spermatogenic cell is roughly the same across species (Harvey and Harcourt, 1984). However, although male chimpanzees are only about a quarter of the weight of male gorillas, their testes are almost four times heavier. This is in harmony with other reports of enhanced testes size among males of species in which females copulate with more than one male during a single oestrus (Primates: Harcourt et al., 1981; Cervids: Clutton-Brock et al., 1982).

It is clear that the male who is able to impregnate several females and continue to display with undiminished vigour is likely to be attractive as well as effective and to respond readily to females who are obviously receptive (Trivers, 1972). Harvey and Bennett (1985) have also pointed out that females might be selected to mate with more than one male in species in which there is already an element of sperm competition. Indeed, this would seem to favour a female attempting to mate with many males during a single oestrus. She may thereby increase her chance of being impregnated by a male who is effective at sperm competition and so transmit this ability to her sons. Sexual swellings are an obvious advertisement of a female's receptive condition and it seems pertinent that

they are restricted to species with multi-male breeding systems (Clutton-Brock and Harvey, 1976; Harvey and Bennett, 1985). However, they are unlikely to have any bearing on her body size. Equally, the comparison between chimpanzee and gorilla males shows that post-mating selection for large testes need not be particularly linked to large male body size.

1.4.4. Niche expansion

The argument in favour of niche expansion as a determinant of sexual size dimorphism is clearly circular, since if one sex is significantly larger than the other then there is almost bound to be dietary divergence. For instance, large males may be unable to reach the young and more nutritious leaves located at the ends of branches and enjoyed by females. As an extreme example, the male orang-utan, on account of his weight, must range between feeding trees terrestrially; he clearly cannot gain access to the same arboreal resources utilised by the female. Male North American weasels are less able than the smaller females to pursue rodents down burrows (Simms, 1979), a problem they share with the male stoat, Mustela erminea (Erlinge, 1981). Yet these observations could easily be secondary consequences of body size differences due to other causes and merely reflect a divergence in male and female body size. Moreover, they could as readily be the result of a

female decrease in size as of a male increase. In addition, although there is evidence from some bird species that dimorphism in beak size and shape has evolved to increase the food available to a monogamous pair (Selander, 1966), no similar effect has been observed among mammals. Moreover, the prediction would surely be for sexual dimorphism to be associated with monogamy, whereas, in practice, it is the more polygynous species which tend to be dimorphic (Clutton-Brock et al., 1977; Harvey and Bennett, 1985). Dittus (1979) remarked that in baboons, predation on other vertebrates is almost exclusively the preserve of the large males. It may be that these animals have succeeded in increasing the carrying capacity of their environment with respect to themselves by managing to exploit a new resource, not available to other members of the species.

1.4.5. Anti-predator defence

This further male-oriented explanation hinges on the argument that bigger males can better protect the social unit (Altmann, 1974; Bramblett, 1976; Crook, 1972; De Vore and Washburn, 1963, Eisenberg et al., 1972; Gartlan and Brain, 1968; Hladik, 1975; Kummer, 1971). It is certainly true that, for primates, the role of the large male both as intraspecific guardian of the social unit and inter-specific protector against predation has been well

documented in particular cases, especially for various baboon species and for patas monkeys (e.g., Altmann, 1974; De Vore and Washburn, 1963; Kummer, 1971) whilst Altmann has also observed, with respect to baboons, that "it is rare to find females without males although the converse is not true". Nevertheless, these reports do not settle the fundamental evolutionary question - whether these males were initially selected for large size to defend the social unit or merely fulfilled this role because they had already been size selected for some other reason. In addition, the protective activities engaged in by some males might simply have enhanced an existing trend towards an increase in body size rather than constituting its primary cause. However, the cardinal objection to the predator defence argument as the mainspring of sexual size dimorphism lies in its failure to explain why adult males of forest Cercopithecus should be much larger than females, although they play no active role in group defence (Struhsaker, 1969). The same author's report of the rarity of defensive behaviour by sexually dimorphic adult males of the more terrestrial, savannah-dwelling vervet monkey, Cercopithecus aethiops, likewise runs counter to the claim that sexual dimorphism in body (and canine) size is primarily related to group defence.

1.4.6. Divergent energy strategies

The exigencies of pregnancy and lactation mean that an adult female must be able to obtain more resources than would be needed for her own body maintenance alone. An adult male also uses additional energy in competing for a mate; this is the hidden cost associated with his reproductive effort. Both sexes invest heavily in reproduction, but according to their different roles and needs, so that their respective cost-benefit equations are likely to differ profoundly. It seems entirely plausible that the "divergent energy strategies of females and males may be the primary factor underlying sexual size dimorphism and that male strategies in competition for females and anti-predator defence may be conditional on this" (Martin, 1980a).

1.5 THE PRESENT APPROACH

It is taken for granted in human societies that men are, on average, slightly taller, larger and heavier than women, notwithstanding a considerable overlap in their respective weight distributions. However, this is not a universal biological fact. Among mammals in general the intersexual size difference within a single species is not always in favour of the male and ranges from leopard seals, with the female 20% longer and correspondingly heavier than the conspecific male, to orang-utans with the male more than twice the size of his mate.

Despite this variety of expression, in terms of both direction and magnitude, with a few notable exceptions (e.g., Clutton-Brock et al., 1977; Downhower, 1976; Ralls, 1976, 1977), most research has centred on identifying selection pressures which might be responsible for the increased size of the larger sex. The comparative nature of this finding has consistently been overlooked. The large males of sexually dimorphic primate species are typically referred to as bigger than the females, although it would be equally valid to describe females of such species as being smaller than the males. Perhaps this style of reporting has coloured the general perspective and resulted in so little attention being given to the possible outcome of adaptive pressures acting on the female. Yet it seems equally valid to seek an explanation of sexual size dimorphism in terms of the benefits which might accrue to the smaller sex by virtue of a decrease in overall body size. Indeed, it will be argued here that, in certain environments, females might gain from the earlier attainment of sexual maturity at the expense of a reduction in adult body size.

Both sexes are presumably subject to selection for optimal size and the outcome could well differ radically between them on account of their very dissimilar energetic

and physiological requirements. In view of these, it is almost more remarkable that males and females of some species favour the same adult body weight. Whilst it is conceivable that intersexual differences in both size and form could arise for non-adaptive reasons and persist if not actually disadvantageous, this would seem to be an improbable explanation. Since body size may well be a critical factor in survival it is not likely to be determined as an indirect result of other processes.

Taking account of these considerations, the following discussion of sexual size dimorphism concentrates on the divergence between male and female strategies without ascribing a dominant role to selection on either one of the sexes. The first chapter explains the nature and sources of the data which formed the basis of the enquiry. This is succeeded by a discussion of the statistical techniques employed in the subsequent analyses and includes a brief introduction to the concept of allometry.

The evolutionary implications of sexual size dimorphism are unlikely to be understood without first discovering why, when and how it occurs. The answer to the first of these questions must lie in the selective benefit a change in adult body size might confer and may well differ between the sexes. The nature of such an advantage

is most likely to be determined by considering the different constraints within which males and females fulfil their respective life histories. This enquiry forms the subject matter of chapter 3. The logical sequel was an examination of the ontogeny of intersexual size differences. Chapter 4 explores the manner in which male and female growth trajectories typically diverge, and seeks to establish whether sexual size dimorphism between adults arises in consequence of a faster rate or a longer duration of growth in the larger-bodied sex, or possibly through a combination of both of these. The findings are then considered in relation to energetic needs and maternal investment. They form an essential precursor to any attempt to clarify the origins of sexual size dimorphism.

As previously remarked, there is a disturbing degree of circularity in most theories of sexual size dimorphism. This problem is inherent in many biological situations since it is seldom possible to achieve a neat separation between dependent and independent variables. Indeed, the distinction is often non-existent, since such systems function as a whole and their component elements are interdependent.

The present research encountered the same obstacles.

However, these were countered by exploiting anomalies in the allometric scaling of brain weight and molar tooth area with adult body weight. Chapter 5 presents the findings on brain weight relative to overall body size, together with an examination of intersexual differences in both the absolute size and organisation of the brain. Chapter 6 focuses on the dental evidence, which was found to corroborate the inferences based on the scaling of the brain. Chapter 7 offers a synthesis and comment on the material presented in the earlier chapters, including their implications for future research.

CHAPTER 2

METHODS

2.1 OVERVIEW

The present research focuses on both intersexual and intrasexual differences which might yield clues as to the likely origins of sexual dimorphism. Numerous previous studies have examined variables such as brain size and lifespan in relation to body size. The methodology adopted here differs in that data on males and females have been separated prior to such analysis. At the same time, a deliberate attempt was made to discover and appraise attributes (such as maternal investment) that differ within sex according to degree of dimorphism. In addition to classifying the data by sex, species were also assigned to subgroups according to the degree of sexual dimorphism evinced. Decomposing the data in this way seemed to offer the best chance of identifying the features which differ between monomorphic and dimorphic species as well as those that are common to both groups. By viewing these in an evolutionary context it was hoped to gain a better understanding of the adaptive significance of sexual dimorphism. The formal analysis then depended on

establishing a sound data base and selecting those statistical procedures that seemed best suited to the nature of the enquiry.

2.2 MONOMORPHIC AND DIMORPHIC CATEGORIES

In order to classify the data, relevant categories had first to be defined in unambiguous terms. Following the decision to focus on sexual dimorphism in adult body weight (see page 14), a criterion was needed for designating species as either 'monomorphic' or 'dimorphic' in terms of this particular dimension. For purposes of analysis and interpretation, it was decided that any species for which the average adult male body weight exceeded that of the female by at least 15% would be designated as 'dimorphic'. The choice of 15% as the critical value was based on the following considerations. Although every effort was made to ensure reliability and consistency in the data used (see 2.4.1), average body weight data for males and females of some species were, of necessity, based on small samples (3 or 4 animals of each sex) or in rare cases single individuals. Even within sex and within species, adult body weight is subject to considerable variation. This inevitably leads to high standard errors in estimates of mean body weights for each sex taken separately and to an even greater degree of variability in the corresponding ratio estimates of male

to female body weight. The use of a 'cut-off point' of 1.15 appeared to cope effectively with the problem of incorrectly classifying a monomorphic species as dimorphic merely on account of sample variability in male and female body weights.

The premise that a correct classification exists is supported by detailed descriptions contained within several qualitative studies. Unfortunately, these minutely documented field studies seldom include 'hard' data on actual body weights, although they commonly report both sexes as being the same size. For example, Kingdon (1971-1982), in his careful observations of East African mammals, frequently refers to adult body weights (by sex) lying within a specified range, or alternatively quotes average weights for males and females without reference to sample sizes. Body weights of individual animals are not reported. Such quantitative limitations make it difficult to generate a classification which is broadly consistent with available information drawn from other sources. However, the criterion of 1.15 seemed to serve this purpose; it had the particular merit that, whereas several male to female weight ratios lay in the range 0.96 to 1.07, none was greater than 1.07 but less than 1.15 (see Table 2.1). The index value of 1.15 should not, of course, be ascribed any profound biological significance.

TABLE 2.1

FREQUENCY DISTRIBUTION OF MALE TO FEMALE BODY WEIGHT RATIOS FOR PRIMATES

RATIO	FREQUENCY
0.90 - 0.94	-
0.95 - 0.99	4
1.00 - 1.04	6
1.05 - 1.09	5
1.10 - 1.14	-
1.15 - 1.19	6
1.20 - 1.24	6
1.25 - 1.29	2
1.30 - 1.34	4
1.35 - 1.39	2
1.40 - 1.44	5
1.45 - 1.49	2
1.50 - 1.54	1
1.55 - 1.59	1
1.60 - 1.64	-
1.65 - 1.69	2
1.70 - 1.74	2
1.75 - 1.79	3
1.80 - 1.84	3
1.90 - 1.89	2
1.95 - 1.99	2
2.00 - 2.04	2
2.05 - 2.09	-
2.10 - 2.14	1
2.15 - 2.19	-

The present study focuses on sexual size dimorphism only in relation to those species for which the male is the larger sex. There are many mammal species for which females are heavier than males (Ralls, 1976), but these are not, typically, primates. Although females have been reported as larger than males for a few primate species, the intersexual size difference is either slight or controversial or both. For example, on the evidence of a mixture of published and unpublished data, Ralls (1976) concluded that females are larger than males for all species of spider monkey. The present study corroborated this finding for Ateles fusiceps and Ateles geoffroyi, but not for Ateles paniscus. The current data yielded male to female body weight ratios of 0.97, 0.98 and 1.06 respectively, for these three species. However, it was not possible to assess the significance of the results since the sample sizes were not known. Ralls (1976) also noted that female body size exceeded male body size for two species of tamarins. This is in harmony with the present finding of male to female body weight ratios of 0.97, 0.98, 0.95 and 0.96 for Saguinas fusicollis, S.geoffroyi, S.midas and S.oedipus repectively. Once again, sample sizes were unavailable. Among the lesser apes, females of the single species Hylobates concolor appeared to be 4% heavier than males. It has frequently

been asserted that female marmosets are larger than males, but the published results are conflicting. Lunn (1981) has summarised the arguments thus: "on a body weight basis the male marmoset is said to be heavier than the female (Napier and Napier, 1967), the same weight (Turton et al., 1978b) or lighter (Shultz, 1969)". Lunn's own meticulous research revealed no significant size difference between the sexes. Indeed, the extent of the sexual size dimorphism is relatively slight even among primate species for which the female is genuinely the heavier sex. Thus, the male to female body weight ratio is never less than 0.95 and only reaches this level for a single species. Bearing in mind the 1.15 cut-off point adopted for dimorphic species with males heavier than females, those species with females as little as 5% larger than males have been included in the monomorphic category. There are also many non-primate mammals for which the male to female weight ratio is less than 0.95. These range in body size from several species of mice, hamsters and bats through dolphins and seals to whales. However, since the current research is directed mainly towards an enhanced understanding of sexual size dimorphism in the Order Primates, an examination of the concomitants of this reverse form of intersexual size difference is beyond the scope of the enquiry.

2.3 QUANTIFYING SEXUAL SIZE DIMORPHISM: AN INDEX FOR ILLUSIONS

The intensity of sexual size dimorphism (SSD) is frequently expressed either as the difference between male and female adult body weights or as the ratio of male to female adult body weight. The relation between the degree of sexual size dimorphism and the adult body weight of a species is then typically explored in terms of the correlations that emerge between the favoured index and body weight. Adult body weight is usually estimated as the average weight of both sexes or, perhaps more commonly, by that of the adult male. Yet this approach ignores the fact that, irrespective of biological reality, the standard definitions of sexual size dimorphism must inevitably generate a level of correlation between these two entities. In effect, it is the correlation of Y-X or Y/X with either Y or (Y+X)/2 that is under scrutiny.

There are probably very sound biological reasons why the degree of sexual size dimorphism tends to increase with overall body size and, in particular, why there is likely to be a minimum weight threshold which must be attained before a marked divergence in male and female adult body weights becomes a feasible option (see pages 77-78). Moreover, since there is an abundance of small, monomorphic species, the impression of a strong positive correlation between level of SSD and overall body weight

will be gained, although this apparent association may rest primarily on the contrast between the presence and absence of SSD, rather than on a more comprehensive examination of its varying intensity. Indeed, some quite striking anomalies emerge when focusing on the strength of the association among similar species within a restricted range of body sizes. For example, Cercopithecus aethiops shares the same average adult body weight with Cercopithecus pygerythrus, yet the former has a male to female body weight ratio of 1.41 and the latter 1.78, a difference of more than 25% (Data: R.D. Martin & A.M. MacLarnon; pers. comm.)

Using the definitions cited, efforts to demonstrate a correlation between SSD and body weight in quantitative terms are inherently unsound, despite the confidence intervals and significance levels which abound in most presentations. Results couched in the formal language of statistics without due deference to the necessary conditions and assumptions that underly its techniques are at best misleading, at worst dangerous, since they create an illusion of rigour which is no more substantial than the Emperor's new clothes.

Once a biological index has been defined, it tends to take on a life of its own and to be subjected to extensive analysis, unmindful of its component elements. The index

of sexual size dimorphism is almost uniquely incalcitrant in this respect. It is a function of two variables, at least one of which is, at the same time, indispensibly required as a point of reference. Moreover, to further compound the problem, the two relevant variables are likely to be highly correlated with each other. In the case of sexual size dimorphism, X and Y are not remote abstractions - they denote male and female adult body weights within a single species. A simple estimate of the correlation between the body weights of adult males and females for 55 primate species amply illustrates the degree of association between these two entities ($r = 0.97$, $p < 0.001$) and properly expresses the evolution of adult body size according to phylogeny, species and sex, in that order.

How then should these confounded relationships be examined? Is it possible to probe beyond the inbuilt correlations which undermine so many studies of sexual size dimorphism? An essential prerequisite is surely to assess the level of correlation likely to arise as an artefact of the definition of sexual size dimorphism adopted. Subsequently, if empirical data merely yield a correlation of the same order, the association is biologically void and reflects only the mathematically confounded definitions of the key entities. On the other

hand, if a higher correlation is obtained than would be predicted on the basis of such contaminated definitions, this would then merit more serious consideration as a possible expression of an evolutionary trend. Such an approach may seem somewhat unscientific and it certainly has no pretentions to statistical rigour; nevertheless, it is preferable to ignoring the issue altogether.

Unfortunately, the relations between some of the more complex measures of sexual size dimorphism and species' body weight are not amenable to direct analysis, although they can be explored by computer simulation. However, the simplest definition of sexual size dimorphism, that of male body weight minus female body weight, taken in conjunction with male body weight can be examined algebraically:

Let X= weight of male $\quad \bar{X}$= mean X $\quad x = X-\bar{X}$

Let Y= weight of female $\quad \bar{Y}$= mean Y $\quad y = Y-\bar{Y}$

Let $Z = X-Y$ $\quad \bar{Z}$= mean $Z = \bar{X}-\bar{Y}$ $\quad z = Z-\bar{Z}$

Then the correlation of Z with X is denoted by r_{zx} where

$$r_{zx} = \Sigma zx / \sqrt{(\Sigma z^2 \Sigma x^2)}$$

Substituting $z = x-y$, then r_{zx} can be rewritten as:

$$r_{zx} = (\Sigma(x-y)x) / \sqrt{(\Sigma(x-y)^2 \Sigma x^2)}$$

$$= (\Sigma x^2 - \Sigma xy) / \sqrt{(\Sigma(x^2 - 2xy + y^2)\Sigma x^2)}$$

$$= (\Sigma x^2 - \Sigma xy) / \sqrt{((\Sigma x^2 - 2\Sigma xy + \Sigma y^2)\Sigma x^2)}$$

Now, in the absence of any correlation between X and Y (which is certainly untrue in the present instance when X and Y denote male and female body weights within a single species), then $\Sigma xy = 0$, so that r_{zx} becomes:

$$r_{zx} = \sqrt{(\Sigma x^2 / (\Sigma x^2 + \Sigma y^2))}$$

$$= 1/\sqrt{(1 + \Sigma y^2 / \Sigma x^2)}$$

Moreover, it follows that if X and Y have approximately the same variance (a most unlikely premise for a size dimorphic species), then $\Sigma y^2 / \Sigma x^2 = 1$.

It should be noted that each of the above assumptions would tend to reduce the value of the expression for r_{zx}. Yet it remains at a level that would be accepted as 'significant' for even quite small samples. Thus:

$$r_{zx} = 1/\sqrt{(1+1)} = 1/\sqrt{2} = 0.71$$

This result would be associated with a probability of less than 0.05 for a two-tailed test with n=8.

With X (perhaps a larger male body weight) twice as variable as Y, then the correlation coefficient between Z and X is increased to:

$$r_{zx} = 1/\sqrt{(1+0.5)} = 1/\sqrt{1.5} = 0.82$$

This analysis was corroborated by computer simulations, with X and Y generated as random numbers and hence uncorrelated. The results from 50 replications, each of 200 simulated observations, are given in Appendix 2.1, together with a listing of the simulation program. For X and Y generated with approximately equal variances a mean value of 0.71 was obtained for r_{zx}, whilst with X twice as variable as Y the mean value of r_{zx} increased to 0.81.

Alternatively, suppose that X and Y are perfectly correlated, with $r_{yx} = 1$. Then $r_{yx} = \Sigma xy/\sqrt{(\Sigma x^2 \Sigma y^2)} = 1$, so that the following relation obtains for Σxy:

$$\Sigma xy = \sqrt{(\Sigma x^2 \Sigma y^2)}$$

Substituting this expression for Σxy in the formula for r_{zx} leads to $r_{zx} = 1$. Thus, if X and Y are perfectly correlated, so then are X and Z, a finding confirmed by simulation.

Of course it remains intrinsically likely that sexual size dimorphism will be less pronounced in smaller species, simply because small animals have less leeway to differ (see pages 77-78). The present analysis does not undermine this intuitive judgement. It merely cautions

against ascribing statistical significance to results derived from contaminated variables.

Computer simulations were also carried out to examine the association of X/Y with both X and (X+Y)/2. These represented the common practice of measuring dimorphism as the ratio of male to female adult body weight and investigating this in relation to the adult body weight of either male or female, or to the average adult weight of the species. These two entities yielded mean correlation coefficients of 0.46 and -0.12 respectively. The mean correlations between X and Y were again zero ($r < 0.00$).

The foregoing analyses show that it is inherently unsound to read too much into correlational data which have not previously been screened for inbuilt defects. Structural links may be present in the source material, depending on the manner in which the key variables have been defined.

This complication is central to any examination of the allometry of brain size. However, brain weight represents a relatively small proportion of adult body weight, so that the brain weight component of total body weight

should not unduly distort the results. A computer simulation even with Y ('brain weight') set at 30% of the order of magnitude of X ('body weight exclusive of brain weight') yielded a correlation of only 0.30 between Log(Y) and Log(X+Y). Since the correlations which emerge in the interspecific analyses of actual data for body and brain weights are so much higher, with r typically greater than 0.90, the inclusion of brain weight in estimates of overall body weight should not detract from inferences based on allometric scaling of the brain. The problem did not arise in connection with the other variables investigated.

2.4 DATA COLLECTION

Data were obtained from published collections (e.g., Altman and Dittmer, 1972; Corbet and Southern, 1977), by personal observation and through the generosity of many individuals who communicated previously unpublished material. In addition, an extensive literature search was undertaken, and data abstracted from a wide variety of source papers (see Appendices 2.2-2.4).

2.4.1 Weight data

Body weights were required for males and females at birth, at various developmental stages and at full adulthood, together with the brain weights of mature males and females. Because of the wide variety of sources used,

the available data were necessarily of uneven quality. Information relating to animals of unknown or uncertain sex could readily be excluded, but it was less easy to be sure that none of the entries related to subadult, sick or obese individuals. To mitigate this problem, the median was adopted as the most appropriate measure of the average body or brain weight for small samples ($n < 10$). Larger samples were scanned for extreme values, which were then discarded, and the mean of the remaining data was adopted as the best average for the species. However, in some instances, an average value alone was given, without reference to the sample size on which it was based. Such data have occasionally been included, but only as a last resort, in the absence of anything more reliable.

2.4.2 Age at sexual maturity

It was difficult to obtain consistent estimates of this parameter. Some authors do not clarify whether they are referring to age at menarche, age at first conception or age at first reproduction when they quote female age at sexual maturity. It is sometimes equally unclear whether age of actual or potential first breeding is being cited for males. In so far as possible, corroborative evidence has been sought to resolve these problems. Nevertheless, an element of uncertainty remains, which is likely to increase the level of unexplained variation in subsequent

statistical analyses.

2.4.3 Lifespan

The paucity of data regarding lifespan, and the frequent failure to report whether an animal was male or female, made it impossible to achieve a breakdown by sex on this dimension.

It was decided to adopt maximum recorded lifespan, in preference to average lifespan or life expectancy, as the measure of longevity for a species. The choice was virtually dictated by the scant amount of data that could be secured for either of the alternatives. The lifespan data used in the present study were mainly derived from Jones (1979), who by this time had spent thirty eight years collecting data on the longevity of captive mammals, primarily in zoological gardens.

These data have a particular merit in that they are to some extent controlled for the effects of predation and nutrition and that all the animals would presumably have benefited from similar standards of veterinary care. This may be one of those rare instances when data from captive colonies or individuals is actually preferable to that which might be obtained from wild populations. From an evolutionary perpective, the maximum lifespan achieved by

a single, and perhaps atypical, individual is probably an irrelevance. Yet precisely because it is an extreme value, maximum lifespan is likely to be independent of environmental considerations and to approach the limit for the species. In contrast, life expectancy and average lifespan are both liable to vary in response to local environmental conditions. Consequently, although the selection of maximum lifespan was initially an enforced choice, made in response to the limited availability of other data, this parameter would seem, on closer inspection, to be the most appropriate measure of longevity for a comparative study such as is now being undertaken.

2.4.4 Tooth dimensions

Measurements of the length and breadth of lower first molar cheek teeth were taken from published sources (Swindler, 1976 and Gingerich et al., 1982) and augmented by personal observation of specimens in the British Museum of Natural History (see Appendix 2.5). The specimens selected were from adults of known sex whose live body weights had also been recorded. For the examination of intraspecific variation, the material used was selected from a single geographic location.

2.5 THE ANALYSIS

Allometric analysis was seen as an essential preliminary in the examination of body size dimorphism, since it permits the separation (at least in theoretical terms) of overall trends associated with increasing body size ('scaling effects') from special adaptations of individual species ('grade effects'; see Martin, 1980b). It is clearly extremely important to isolate scaling effects and to compensate for them by some means which will avoid attention being focused on spurious differences which are attributable merely to differences in overall body size of the species concerned. This can be accomplished by the use of allometric techniques.

2.5.1 Allometric scaling

Real organisms are not isometric. That is, with increasing overall size, certain proportions change in a regular manner, and this non-isometric scaling is referred to as allometric. Very many morphological and physiological variables scale to allometric equations of the general form $y = ax^b$, which may also be written as $\log y = b \log x + \log a$. Slope values of $b<1$ reflect an increase that is less than proportional, $b=1$ indicates an isometric increase whilst $b>1$ occurs when the increase is more than proportional. These relations typically have immediate consequences for resource utilisation and may

therefore have far reaching implications for evolutionary change. As an example, metabolic rate scales with b=0.75 (Kleiber, 1961); this permits 'economies of scale', in that although a larger animal will need to consume more food in absolute terms, it will require a lesser intake per unit body weight. In addition, whereas blood volume is always a constant fraction of body mass, the skeleton of a larger animal is proportionately heavier, so that an increase in overall body size may lead to modifications in locomotor habit on account of the different mechanical stresses encountered (Gould, 1966; Schmidt-Nielson, 1984).

Allometric techniques are based on logarithmic bivariate plots of the variable under consideration against body size (e.g., of brain weight against body weight). The 'best-fit' line (see below) reflects the overall trend, or 'scaling effect' for the given characteristic. Departures of individual values from the best-fit line can then be examined and quantified in terms of the logarithmic interval separating a particular point from the line. This displacement affords a convenient index for monitoring the extent to which any observation exceeds or falls short of the expected value for the parameter (e.g., brain size) as predicted by the best-fit line for the relevant body size.

2.5.2 Best-fit lines

There has been extensive discussion regarding the choice of an appropriate best-fit line for allometric analysis (e.g., see Harvey and Mace, 1982; Martin, 1982) and it is still controversial which of the commonly cited lines (regression, reduced major axis, major axis) is most suitable. In practice, if the focal variable is highly correlated with body weight ,that is, with a correlation coefficient r >= 0.98 (see Martin, 1982), then each of the three line-fitting techniques yields virtually the same result, and it is immaterial which is used. However, even for slightly lower correlations the discrepancy between the parameters determined by linear regression and those arising from major axis and reduced major axis becomes appreciable. The slope values derived from linear regression are always lower than those estimated for reduced major axis or major (principal) axis so that, in particular, great care must be exercised if a functional interpretation of the allometric exponent, or gradient b, is required (Martin, 1982). However, this is not a feature of the present research, which is primarily concerned with departures of individual species points from a general scaling trend.

Fitting a linear regression line implies that the variation is concentrated in the Y-variable and that the

X-variable can be measured accurately. In the context of the present study, there is no reason to assume that body weight can be estimated with less error than brain weight, nor, at a subsequent stage in the analysis, that lifespan and age at sexual maturity are subject to differing degrees of error. For these reasons, the current work makes use of the major or principal axis, which allows for errors in both Y and X variables.

However, the choice of an appropriate line-fitting technique is not sufficient in itself to enable the best-fit line to be unequivocably determined. There is a special pitfall inherent in allometric analyses based on bivariate plots. In some cases the points may clearly fall into separate 'grades'. For instance, primates tend to have longer lifespans than most other mammals and hence give rise to a series of points lying above those of other mammals when represented by a logarithmic bivariate plot of lifespan against body weight. In such a situation, it is no longer biologically justifiable to determine a single best-fit line for the data. Furthermore, if points belonging to the higher grade of the plot have a greater mean body weight than those of the lower grade, a single best-fit line estimated for all the data together will have an artificially elevated slope. This will accordingly distort the departures of individual points from the line,

by causing 'expected' values to be overestimated for larger-bodied species and underestimated for species of smaller body size. As a consequence, conclusions based on an analysis of the residuals, or indices, will effectively be invalidated.

To resolve this difficulty, bivariate plots of all pairs of variables were carefully examined for evidence of grade distinctions which might contaminate the results of allometric analysis. In some instances, the existence of grades was revealing in itself (e.g., in relation to maternal investment, see page 147), and the points emerged as clustered about two parallel lines. At other times, the presence of grades posed a handicap and the problem had to be averted by concentrating the analysis upon species drawn from a single grade. Because of the limited availability of suitable data, most of the calculations could not be repeated for several different grades, taken individually. As a result, some of the more sensitive analysis was restricted to simian primate species. This unavoidably led to a reduction in sample size and some loss of generality in the the overall findings, since it restricted the population under consideration.

2.5.3 Statistical procedures

The respective allometric relations between brain

weight, lifespan and age at sexual maturity were examined, as well as the interactions between these major variables. The work on skeletal material investigated the scaling of cheek tooth dimensions with body size or with skull length in the absence of body weight data. Inferences were made on the basis of Pearson product moment correlation coefficients, whilst partial correlations between the key variables were also estimated. These enabled the relations between any two variables to be isolated from the influence of other confounding factors. Group means were compared using the standard normal distribution or student t-tests, as appropriate. The difficulties which were sometimes encountered in making use of these statistical procedures are described in the context in which they occurred.

Calculations were variously performed using purpose written programs (coded by the author) and standard software packages (e.g., SPSS, MINITAB, SORT and QUERY). These were implemented on DEC-10 and IBM main frame computers in addition to a BBC micro-computer.

Sample sizes used in the analyses of particular variables unavoidably fluctuated to some extent, even within sex, on account of differences in the spectrum of information available for individual species. However,

such sample size differences have been allowed for in evaluating the significance levels of the results. There remains a much more intractable problem, relating to the manner in which the data were obtained.

2.5.4 The sampling frame

When quantitative techniques are used, it is essential to ensure that the conditions obtaining are consistent with those demanded by the particular test employed. The choice of a statistical procedure implies both the recognition and acceptance of the assumptions underlying the mathematical model from which it derives. If these are violated, then the results of all subsequent analyses may be quite meaningless (see 2.3). In a similar context, Harvey and Mace (1982) cited the problems inherent in obtaining statistically independent data points at a chosen taxonomic level, a difficulty that has been encountered at various stages in the present research.

Thus, the occasional examples drawn from avian studies have only been used to illustrate the influence of size on survival and in discussing strategies of delayed breeding. All the quantitative analysis has been confined to the class Mammals, and most of it to the order Primates. For some analysis it has even been necessary to

further restrict the sample to individual species drawn from the suborder Anthropoidea. This calls into question whether the data points for such phylogenetically related animals can be regarded as genuinely independent. At the same time, it was elected to use species, as opposed to family or generic estimates for comparing relations between variables. This decision was reached for two reasons, one practical, the other theoretical. The use of species data was partly dictated by the need to avoid prohibitively small samples. It was also favoured because some of the variables under scrutiny (e.g., relative brain size and age at first reproduction) exhibit a degree of variability within a family which would render a single estimate of average meaningless in biological terms. Even at a generic level, there tends to be considerable variation in precisely those characters which are the primary focus of the present research. However, it is hoped that the level of variation between species within a single genus will help to offset any bias due to the uneven representation of genera in terms of numbers of species included in the sample.

There remains the rather disturbing nature of the means by which the data were selected. It cannot be claimed that these data represent a simple random sample from any population. They simply comprise the best

material that could be obtained for a miscellaneous assortment of species for which the required information was available. However, since all subfamilies are represented, it may perhaps be assumed that those species for which sufficient data were available do not differ in any important respect from those excluded from the sample. On the strength of this assumption, the results deriving from the analyses that follow may reasonably be expected to offer a valid approximation to the truth.

CHAPTER 3

SEXUAL DIMORPHISM AND LIFE HISTORY STRATEGIES

3.1 OVERVIEW

The role of life history as one of the determinants of sexual size dimorphism has recently been challenged (Cheverud et al., 1985, 1986). It consequently seems important to establish its relevance in general terms prior to engaging in a more detailed analysis.

Cheverud and his colleagues presented a wealth of material on the genetic transmission of intersexual size differences, demonstrating how variance differences between the sexes can lead to the evolution of sexual dimorphism in a character even when selection has the same intensity in both males and females. They concluded that: "we would expect selection on size alone, equivalent in both sexes, to be a potent force for producing sexual dimorphism" since in primates, for a wide variety of features "even after correction for scale, males tend to have higher phenotypic standard deviations (PSD) than females (PSD male = 1.5 x PSD female)".

Cheverud and his associates also investigated the intensity of sexual dimorphism in body weight in relation

to size, mating system, habitat and diet. From their analysis they inferred a model in which the major variation in sexual size dimorphism was ascribed to phylogenetic inheritance and body size with life history relegated to a very peripheral role. However, this interpretation tends to emphasize the general at the expense of the particular. Because it deals in 'average' effects and 'proportions' of explained variation it tends to gloss over individual anomalies. For example, why should two cercopithecines (C.aethiops and C.pygerythrus), of approximately the same average adult body weight (4175g and 4200g respectively) and so alike that they were previously regarded as a single species, exhibit such contrasting degrees of sexual size dimorphism? The ratio of male:female adult body weight is 1.41 for C.aethiops and 1.78 for C.pygerythrus, a discrepancy of more than 26%. The arguments for advancing phylogeny and size as the causative factors in the ontogeny of sexual size dimorphism are unconvincing. Each must have contributed to the scaffolding of opportunities and limitations which culminates in differential male and female adult body size, but that is all. In addition, to herald phylogenetic inertia as the root cause of sexual size dimorphism has very limited explanatory potential. It merely translates the problem to an earlier period in evolutionary time; for unless sexual dimorphism is assumed to have been the

prevalent ancestral condition, a most unlikely premise (see pages 192, 194), then intersexual body size differences must have arisen during the course of earlier primate radiations. To assert that a species is sexually dimorphic because so, predominantly, were its closely related predecessors does nothing to illuminate the question of why the phenomenon arose in the first place. It serves instead to highlight the dangerous persuasiveness of arguments which hinge on 'it is because it was' to the detriment of further understanding. Moreover, variation in the degree of size dimorphism between related species suggests that even when the effects of phylogeny and size have been removed there will remain much to account for in the ontogeny of sexual size dimorphism. Intersexual differences in life history characteristics may be key elements in solving the puzzle.

Life history variables are fundamental to demographic processes. The rates at which animals reproduce, die and migrate determine the demographic structure of a population. This is important because, amongst other things, population density affects resource availability whilst the age and sex classes and the social groups into which these are organised influence the benefits accruing from various alternative strategies. In particular, breeding success is conditional on the availability of a

suitable mate, and long term fitness depends on reproducing without incurring a damaging penalty in terms of procuring future offspring or risking premature or even present mortality. The impact of these risks, and the attendant opportunities, will inevitably differ between the sexes. In addition, males and females appear to differ in their energetic needs (see 4.4), whilst an individual animal's experience of the environment is further mediated by its social status, which is again, presumably, sex-dependent. Each of these considerations would be likely to promote sexual size dimorphism, which perhaps calls into question why some species are monomorphic.

Life history and demographic variables are so closely enmeshed that it is virtually impossible to distinguish between cause and effect. This is equally true of any attempt to unravel the evolutionary tangle which has promoted sexual size dimorphism in some species but not in others. Evolutionary change is the outcome of a dynamic interaction between selection pressure and adaptive response, both mediated and confounded by genetic variation. Thus, genetic variability, whilst providing a mechanism for change which may be 'fixed' if it proves advantageous, may also lead to nonadaptive modifications. This has led Cheverud and his co-workers (1986) to identify size as "a nonadaptive factor in the evolution of

sexual dimorphism, in that direct selection on size itself will result in the evolution of sexual dimorphism for size if the additive genetic variances of the sexes differ". They further propose that "additive genetic variances may become different in the two sexes if stabilising selection or the phenotypic effects of mutation differ in magnitude between the sexes". Yet the existence of these genetic possibilities does not, in itself, prescribe a unique path by which males and females have attained different adult body sizes. Lewontin's (1985) comment that "the role of population genetic theory is not to predict evolution but to delineate the prohibited and the possible" seems pertinent. In particular, the inference that an increase in the overall body size of a species has carried in its wake a passive weight differential between the sexes is hard to accept. It conflicts with the concept of size as a fundamental element in the equilibrium which an organism must achieve within its environment in order to survive (see 1.2). Indeed, Pickford (1986) noted that the combined weight of mother and infant approximates that of the adult male, which accords with the concept of a target weight for a species (Tanner, 1963). Pickford interpreted this finding as a highly effective strategy for "preserving the balance between the species and the environment".

The study of sexual dimorphism exemplifies the

problems inherent in trying to understand a complex system in which elements that can be identified individually nevertheless function in a composite way so that the whole is more than the sum of its parts. A reductionist approach is doomed to failure since it does not give sufficient prominence to either first or higher order interactions within a set of mutually dependent variables. As a result, information is fragmented and insights denied. Yet to undertake a holistic view requires the simultaneous processing of a diffuse and heterogeneous mass of data, an overwhelming task in the face of evolutionary diversity. The canvas is simply too large to focus on more than a small section at any one time. In consequence, when concentrating on some particular aspect it is virtually inevitable that others will be neglected. In order to resolve the problem, a synthesis of these two approaches must somehow be effected. The relevant variables need first to be identified and considered in terms of their individual nature and influence, with limited concern for the effects of their interactions. Once this has been achieved, then a careful examination of the relations between these component elements should be undertaken. Without this double perspective it will not be possible to make any sense of the system as a whole. Moreover, no perspective whatsoever can be attained without a sound data base.

Unfortunately, a subjective element enters into both the choice of data and the manner in which it is examined. Even the apparently impersonal procedures of statistical analysis are not free from bias, although these tend to convey a spurious impression of objectivity. The methodology and techniques adopted are, to some extent, an expression of personal preferences and competence. It is almost certain that in collecting and sifting large amounts of data evidence will be omitted that would be crucial to other, rival interpretations; those "we dislike or have not thought of"; whilst in analysing the chosen data we tend "automatically to eschew techniques that are unfamiliar or which we find difficult to apply" (Hudson, 1975).

It is important to recognise these limitations in relation to such a widespread and variable phenomenon as sexual size dimorphism. Nevertheless, an explanation is required which, at the very least, is pertinent, internally consistent and in harmony with the available data. In addition, it should lead to an enhanced understanding of the occurrence it seeks to explain, rather than merely being consistent with it. Ideally, it should be "the reading that captures most succinctly what the evidence has to say" (Hudson, 1975).

The real difficulty, of course, lies in attempting to translate these generalities into a working specification for tackling a practical problem. In the particular case of sexual size dimorphism, it seems preferable to allow the evidence to dictate the form of the investigation and to allow this to unfold naturally in response to the available data. It is better to pursue false trails, which can always subsequently be abandoned, than to constrain the enquiry within a straightjacket of preconceived strategies. Moreover, averages must be treated with extreme caution since they are notoriously prone to camouflage inconsistencies and it is precisely such anomalies which must be resolved by any hypothesis seeking explanatory respectability.

It is clearly important to identify those features that distinguish monomorphic species from dimorphic species. Phylogeny may well prescribe the evolutionary possibilities open to an organism, but a species will neither succeed nor even survive if its inheritance is at variance with its environment. If there is any case to be made for the power of the environment in promoting behavioural or morphological change, it is likely to be reflected in the disposition of life history parameters. These, therefore, merit a central role in any serious

attempt to develop a model for the evolution of mammalian sexual size dimorphism.

3.2 SEXUAL SIZE DIMORPHISM AND THE ROLE OF LIFE HISTORY

Gadgil and Bossert (1970) have suggested that "an organism's life history may be looked upon as the resultant of three biological processes, namely maintenance, growth and reproduction". Such statements tend to imply that a successful life history strategy consists in achieving a uniquely optimal allocation of limited resources. Yet there may be no single optimum for a particular species and the optima obtained will almost certainly differ between males and females. There will be further differences between individuals of the same sex at any given time (because of factors such as dominance rank within a group) and within individuals at different times (corresponding to different developmental stages and, especially for females, reproductive status).

The increased nutritional needs of females during pregnancy and lactation are well known. For example, data from a wild elephant population indicate that, irrespective of her requirements at other times, the great need of the lactating female exceeds that of young males during their most rapid growth phase as well as that of

the much larger bulls (Laws, 1975). Dunbar (1977) found no significant difference in the time spent feeding by male and female gelada baboons, notwithstanding the marked sexual dimorphism in both size and weight. In contrast, a study of a monomorphic species of lemuroid, by Pollock (1977), revealed that adult male indri, although the same size as conspecific females and larger than juveniles, nevertheless fed more slowly and for less time than either of these classes as well as being most easily displaced from feeding. Even outside pregnancy, it seems that some adult females may consume more food than males of the same species. Thus, an adult male Sykes monkey required a 10% lower energy input than a non-pregnant adult female, despite the male weighing 40% more (Coelho, 1974). Perhaps adult females of all species typically consume more, relative to their body size, than males of the same species.

It seems likely that, for most species, males and females differ in their nutritional requirements at some stage. For monomorphic species, this may be after the attainment of sexual maturity. Among dimorphic species, intersexual differences in food intake may arise at the same time as the growth trajectories of males and females diverge (see 4.3). However, the life expectancy of an individual of either sex will still depend on its ability

to secure the necessary resources. These may differ in either quantity or quality between the sexes, but this is immaterial. The key determinant of survival is not what is needed, but whether this can be obtained. In this connection, rank is likely to be a major factor in ensuring survival. Indeed, many animals die because they are 'socially' excluded from the food supplies that they so urgently require (Dittus, 1979, 1980). At an even earlier stage, the mortality of unweaned animals of both sexes almost entirely reflects the capacity of an adult female to maintain the appropriate level of maternal investment. This, in turn, is likely to be a function of both the mother's rank and the future return she can expect for her present commitment. These factors have different implications for the survival of her sons and daughters. A high ranking female will have preferential access to resources compared with a subordinate animal. In consequence, for species organised so that females remain in the maternal troop, a dominant mother may subsequently benefit from the support of a vigorous daughter who has inherited her own rank. In contrast, a subordinate female in such a society might gain more by investing heavily in sons. If this enables her adult male offspring to gain in dominance status, outside their natal troop, then the mother enhances her own inclusive fitness (Clutton-Brock, 1982).

Studies of sexual dimorphism in teeth are also indicative of divergent feeding strategies. Harvey et al. (1978) report that female primates usually have larger cheek teeth than expected in comparison with males of the same body size. Cheek teeth especially play a major part in the preparation of food for digestion and feeding differences between the sexes in either dietary characteristics or quantity of food intake would be expected to influence their dental morphology. However, any inferences should be made with extreme caution because of the effects of differential growth trajectories on early maturing components such as teeth. Indeed, the anomalies which arise in relation to such early maturing components are exploited in chapters 5 and 6 as an aid to discovering the evolutionary origins of sexual size dimorphism. Different hypotheses lead to different predictions regarding the allometric scaling of both adult brain weight and molar tooth area. These expectations are conveniently quantifiable and can be used to determine whether selection pressures have operated mainly on males, generating an increase in their adult body size or primarily on females, favouring the attainment of sexual maturity at a smaller overall body size which is then retained throughout adulthood, or whether both of these responses occurred simultaneously.

However, despite the reservations expressed and the attendant difficulties in distinguishing between the effects of actual niche separation and quantity of food consumed, some form of dietary divergence between the sexes seems to be indicated. In addition to the examples already cited, a number of field studies have found sex differences in feeding patterns for several primate species (Chivers, 1977; Clutton-Brock, 1977, Fossey and Harcourt, 1977; Kummer, 1971; Quris et al., 1981; Rodman, 1977; Waser, 1977). Indeed, Gautier-Hion (1980) suggests that in some cases there may be more divergence in dietary behaviour between males and females of the same species than between some individuals of different species living sympatrically.

Since so much of an animal's time is devoted to securing the necessary resources, especially food, differences between the feeding activities of males and females are likely to further accentuate differences in their respective patterns of behaviour. These will then colour both intersexual relations and social structure, becoming powerful mediators of life history strategies.

3.3 REPRODUCTIVE SUCCESS, SIZE AND SEXUAL MATURITY

It seems reasonable that selection for breeding

success should operate independently on both sexes and so might favour divergent traits in males and females.

The number of offspring fathered by a sexually mature male depends essentially on the number of matings he achieves and his level of sperm production. As well as being potentially fertile, he must be able to compete effectively for access to receptive females. In contrast, when adequate resources are available and early breeding is advantageous, female mammals are typically able to start breeding at an earlier age without incurring any additional social costs, since males do not constitute a limiting factor (see also Trivers, 1972). Conversely, a male's long-term benefit may lie in delaying his first reproduction to avoid prematurely engaging in stressful and dangerous conflicts with older and more experienced animals (primates: Crook, 1972; birds: Selander, 1965). He may enhance his ultimate reproductive capacity by conserving his energy until such time as he is more likely to be successful in competing for a mate. The avoidance of unacceptable risks in inter-male competition has also been reported in a study of male intrasexual size dimorphism among red deer, Cervus elaphus (Gadgil, 1972), and is consistent with this interpretation - namely, the postponement of first mating as a risk avoidance strategy. Female choice may also play a part; mating attempts by

young sexually mature gorillas and orang-utans are rejected by the females until these males have acquired their secondary sexual characteristics. It has also been observed that females frequently initiate sexual activity in both birds and mammals.

Throughout the duration of her breeding life, the number of offspring produced by a female mammal is constrained by the exigencies of pregnancy and lactation. An increase in potential fecundity would surely follow an increase in reproductive span, which could, in principle, be achieved by the simple expedient of lowering the age of sexual maturity, provided that this was not negated by an associated decrease in longevity. In fact, a theoretical study by Lewontin (1965) actually demonstrated that a change in the age of sexual maturity is the factor which has by far the greatest influence on reproductive potential. However, earlier breeding is only a viable strategy if both the younger, less experienced mother and her infant can survive. When food is relatively difficult to obtain and its acquisition may involve intraspecific conflict, then the strain of reproduction will inevitably be greater. Moreover, even if she has been able to sustain herself through a successfully terminated pregnancy, a female with a nursing infant is most hampered in competition for limited resources at precisely that period

when her nutritional needs are greatest - her energetic needs may be increased by as much as 50% when lactating as compared with 25% more during pregnancy (Coehlo, 1974). It follows that in situations of scarcity a female may benefit by delaying her first breeding in order to increase not only her own chances of survival but also those of her dependent offspring, which would almost certainly die without adequate maternal care.

Indeed, under some conditions it may even be necessary for both parents to cooperate in order to rear their young successfully. In such circumstances, male and female breeding strategies are more likely to coincide and delayed reproduction may be apparent in both sexes. It has been reported among Mexican jays (Woolfenden, 1975) that, when intraspecific competition is increased by adverse climatic conditions, mature offspring, which have already reached breeding age, remain at the parental nest 'helping' with younger siblings by feeding and protecting them. Under less stringent circumstances these individuals would already have left to form new breeding units (see also Emlen, 1982). A similar pattern of delayed breeding and nurturing behaviour towards siblings is also emphasised among marmosets during periods of environmental stress (Kleiman, 1977) while Moehlman (1979), in her study of blackbacked jackals (Canis mesomeles), noted long-

term pair bonds coupled with a tendency for some offspring to help in the provisioning and guarding of subsequent litters. This may be the 'price' demanded for continuing to live within the parental hunting range even after subsequent mating. In addition, Kingdon (1971-1982, vol. 3: Carnivores) described one or more families of blackbacked jackals living within the same territory as well as groups of six or more unpaired adults and subadults. Moehlman (1986) reported that 24% of known surviving silverbacked jackal pups of both sexes remained on their natal territory, helping in the rearing of siblings from the next litter. They fed, protected and groomed younger brothers and sisters in addition to feeding their nursing mother and defending their home range. Similar behaviour was observed in as many as 70% of golden jackals, Canis aureus. Moehlman ascribes this higher percentage to the greater cost of gaining a territory in the short grasslands inhabited by this species, a view supported by Kingdon's observation that young golden jackals may mature and mate while continuing to share the parental range and den. Predation pressure has possibly led mongoose offspring to delay first breeding and remain in the family group, helping to raise siblings. The immediate reproductive cost is presumably outweighed by the protection afforded by group living in relation to increased survival together with the benefit

to future reproduction deriving from kin selection (Rood, 1986).

However, in other situations it may not be necessary to pay such a penalty in order to breed successfully. It also seems generally feasible that, when this would confer a selective advantage, the age at first reproduction might be lowered by becoming sexually mature at a smaller body size. Age at first breeding is strongly correlated with adult body size, since growth typically ceases once reproductive activity begins. However, this response is likely to be conditional on an initial lower limit to adult body size, perhaps to some extent phylogenetically determined. It may well be that the constraints of a particular morphology dictate a threshold female body size which must be attained prior to reproduction. This would help to explain both the virtual absence of positive sexual size dimorphism (i.e., male larger than female) in very small mammals (indicated by the data of the present study) and also the larger size of females, relative to males, which tends to occur in small species of some taxa.

As a corollary, it might be predicted that the degree of positive body size dimorphism should tend to increase with the average weight of the species concerned. After all, it would be among these larger, non-seasonal

breeders that females would enjoy most scope for an adjustment in the age of first reproduction achieved through a modification of adult body size. Indeed, numerous studies have demonstrated this association for a wide variety of taxa drawn from invertebrates, birds and mammals (Clutton-Brock et al., 1977; Leutenegger and Cheverud, 1982; Leutenegger and Kelly, 1977; Mace, 1979; data of present study). Yet, despite its ready appeal, the generalisation is not without exception and there is a conspicuous lack of correlation between size and degree of sexual dimorphism in respect of the two extremely closely related species of cercopithecine already cited (page 61). Moreover, some of the correlations quoted may be the outcome of using contaminated input variables (see 2.3).

Gautier-Hion and Gautier (1985) inferred a significant association between sexual dimorphism and body weight on the basis of a correlation coefficient of 0.73 obtained from a sample of 7 species. However, since dimorphism was measured as the ratio of male to female adult body weight and species body size as the mean body weight of adult males and females, these entities could conceivably have been correlated by virtue of the manner in which they were defined. This possibility was investigated by carrying out a computer simulation. Samples of size 7 were generated and the correlations between X/Y and (X+Y)/2

examined. It emerged that less than 5% of the 200 simulated samples yielded a correlation coefficient of 0.7 or more, so that Gautier-Hion and Gautier's interpretation of their data appeared to be justified. Nevertheless, without the simulation, their inference would have rested on a somewhat tenuous assumption. The preliminary screening of potentially contaminated variables should ideally be a matter of routine in the course of any quantitative study.

Yet, despite the problems and exceptions, sexual size dimorphism typically increases with increasing body size. This is hardly surprising since, in general, an overall size increase of a species permits the expression of new potentiality (Gould, 1966). Increased size, being correlated with longer lifespan, creates opportunities for greater flexibility in age of maturity and first reproduction. The small mammal is constrained by virtue of its short lifespan; larger mammals can more easily maximise their breeding potential by altering the duration of their pre-reproductive period.

Another salient factor is the seasonality of breeding which is typically a feature of small-bodied mammals. Large animals which are not seasonal breeders can incorporate small scale adjustments into both their age at

first reproduction and interbirth interval. This possibility is denied to individuals that are locked into a seasonal breeding cycle such that any change in reproductive parameters must be of the order of a quantum leap, which is unlikely to be a feasible option. The power of the seasonal constraint may be inferred from observations on interbirth intervals among species that are restricted in this way. For example, female vervets which have not achieved breeding condition at the appropriate time do not become pregnant later in the same year but wait until the following season (Lee, 1984). Since small mammals are typically more limited by the annual cycle of resource availablity than larger mammals, they are also more inclined to reproduce seasonally and are consequently less able to accomplish a reduction in the age of first reproduction. This restriction dispels the potential advantage of a reduction in adult female body size, originally envisaged as a by-product of becoming sexually mature at a younger age and a correspondingly earlier stage on the growth trajectory. Such considerations militate against intersexual size differences in small species and, together with the possibility of a minimum size threshold (particularly of the female), seem to account for the relative absence of sexual size dimorphism among small-bodied mammals.

However, while this line of argument is consistent with the general tendency for sexual size dimorphism to increase with average species body weight (see page 77) it does nothing to clarify the prominent variations in degree of size dimorphism which frequently arise between species of similar average body size. This failure highlights the inherent danger in treating size as an independent variable and ascribing to it a causative role. Size is a potent factor in opening up new possibilities, but acts as a catalyst rather than a reagent. Although mammals must be large enough to have the scope to manipulate their age at sexual maturity, this is a necessary but not a sufficient condition for sexual dimorphism to ensue. Once the size barrier has been breached, then phylogenetic inheritance and direct environmental influences are likely to be the critical factors in determining the degree of sexual size dimorphism attained. It is predictable that different taxa will adapt differently to a common habitat. It is less clear why closely related species living sympatrically should favour widely divergent degrees of sexual dimorphism in adult body size. An understanding of the selective pressures and constraints which have contributed to this finding should yield valuable insights into the phenomenon as a whole.

3.4 POLYGYNY AND MONOGAMY

The association between sexual dimorphism and polygyny has often been noted, but the explanations suggested have typically tended to be male-centred. It seems more realistic to regard sexual size dimorphism as the result of sexually divergent strategies, with both males and females responding dynamically to evolutionary pressures.

On the whole, it seems predictable that sexual size dimorphism, with the male the larger sex, should be most prevalent among fairly large, polygynous mammals with access to relatively plentiful resources (see Clutton-Brock *et al.*, 1977; Clutton-Brock and Albon, 1980) and correspondingly rare under intensely competitive conditions. Monogamy as well as monomorphism should theoretically ensue under circumstances which might preclude the successful rearing of offspring by one parent alone (see Kleiman, 1977). On this basis, monogamous mammal species should be characterised by single births, limited sexual size dimorphism and a relatively long prereproductive period of common duration for both sexes. As a consequence, females might be expected to mature generally later in monomorphic than in dimorphic species. In contrast, polygynous species should probably be dimorphic, with females typically attaining sexual maturity before males and relatively early. Indeed, the

influence of the environment on age at sexual maturity can be inferred from field observations. For instance, the red kangaroo, Megaleia rufa, is reported to reach puberty at 27 months in regions with abundant food but not until 35 months when food is scarce (Glucksmann, 1974). A similar disparity in the mean age at first conception of female vervet monkeys (52.8 months and 68.4 months) has also been linked to variation in the productivity of the environment (P.C. Lee, pers. comm.), whilst a negative correlation between population density and age of first reproduction has been noted for elephants (Laws, 1966).

The prediction that size dimorphism is associated with differences in age at first reproduction, both within and between sexes ought to be open to direct examination (but see pages 103-104). The more fundamental question, whether a reduction in female body size has led to earlier first breeding or whether an increase in male body size has resulted in the postponement of sexual maturation, can only be approached indirectly. An assessment of the ancestral condition, with its evolutionary implications, depends on inference and can only be presented in terms of a balance of probabilities. These are assessed later, in the light of information derived from analyses of brain weights and tooth sizes relative to adult body weights for monomorphic and dimorphic species (see Chapters 5 and 6

respectively). As a preliminary, the techniques of allometric analysis (see 2.5) have been used to control for the effects of differential body size when seeking to probe the interactions between various life history parameters.

3.5 ALLOMETRIC ANALYSIS OF LIFE HISTORY PARAMETERS.

Age at first reproduction and lifespan were selected as key life history parameters common to both sexes. Brain size was also included in the analysis, since it is central to problems of grade distinction (see 2.5.2). The results of basic allometric analyses of the available data, for all mammal species taken together, are shown in Table 3.1 and Figures 3.1-3.4. In every plot there are clear scaling trends. At the same time, despite the highly significant correlations found, there remains a considerable element of unexplained variation in each of the bivariate analyses, with the exception of the relation between brain weight and body weight. Here the unexplained variation is only 8% for females (Figure 3.1 and Table 3.1) and 6% for males (Table 3.1). The association between sexual maturity and body weight leaves a variation of 55% to be accounted for in the case of males and 56% in the case of females. For both sexes, some variation is undoubtedly attributable to shortcomings in the data, (e.g., use of age at menarche rather than age of first

TABLE 3.1

RESULTS OF BIVARIATE ALLOMETRIC ANALYSIS (ALL MAMMALS)

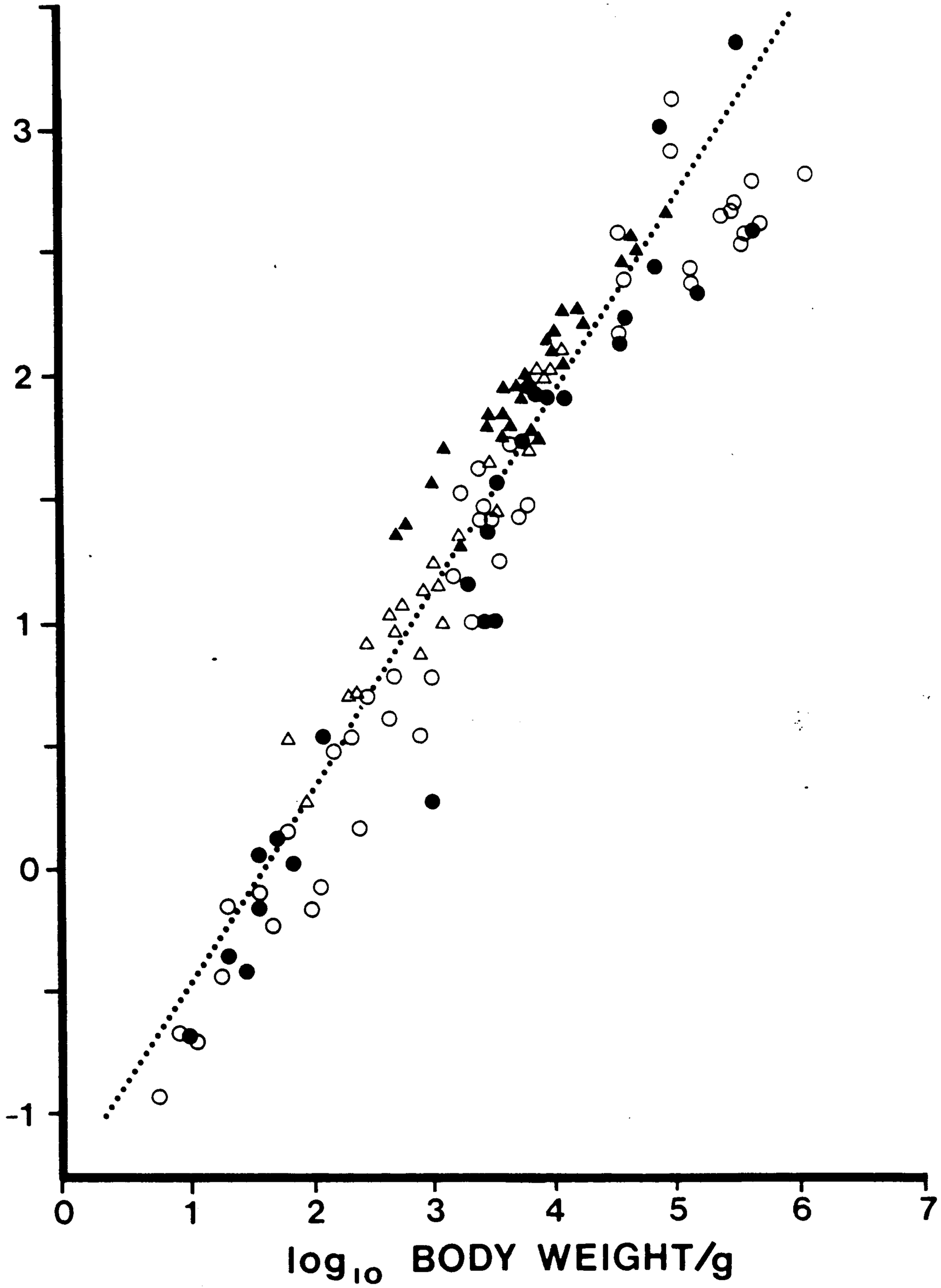
FEMALES

	n	r	r^2	a	b
Brain weight vs. body weight	130	0.96	0.92	-1.28	0.79
Lifespan vs. body weight	104	0.57	0.32	1.65	0.16
Age at sexual maturity vs. body weight	133	0.66	0.44	0.33	0.25
Lifespan vs. age at sexual maturity	79	0.77	0.59	1.37	0.66
Lifespan vs. brain weight	41	0.69	0.48	1.96	0.25

MALES

	n	r	r^2	a	b
Brain weight vs. body weight	155	0.97	0.94	-1.30	0.78
Lifespan vs. body weight	103	0.64	0.41	1.51	0.19
Age at sexual maturity vs. body weight	111	0.67	0.45	0.29	0.26
Lifespan vs. age at sexual maturity	63	0.73	0.53	1.48	0.59
Lifespan vs. brain weight	44	0.69	0.48	1.82	0.29

FIGURE 3.1

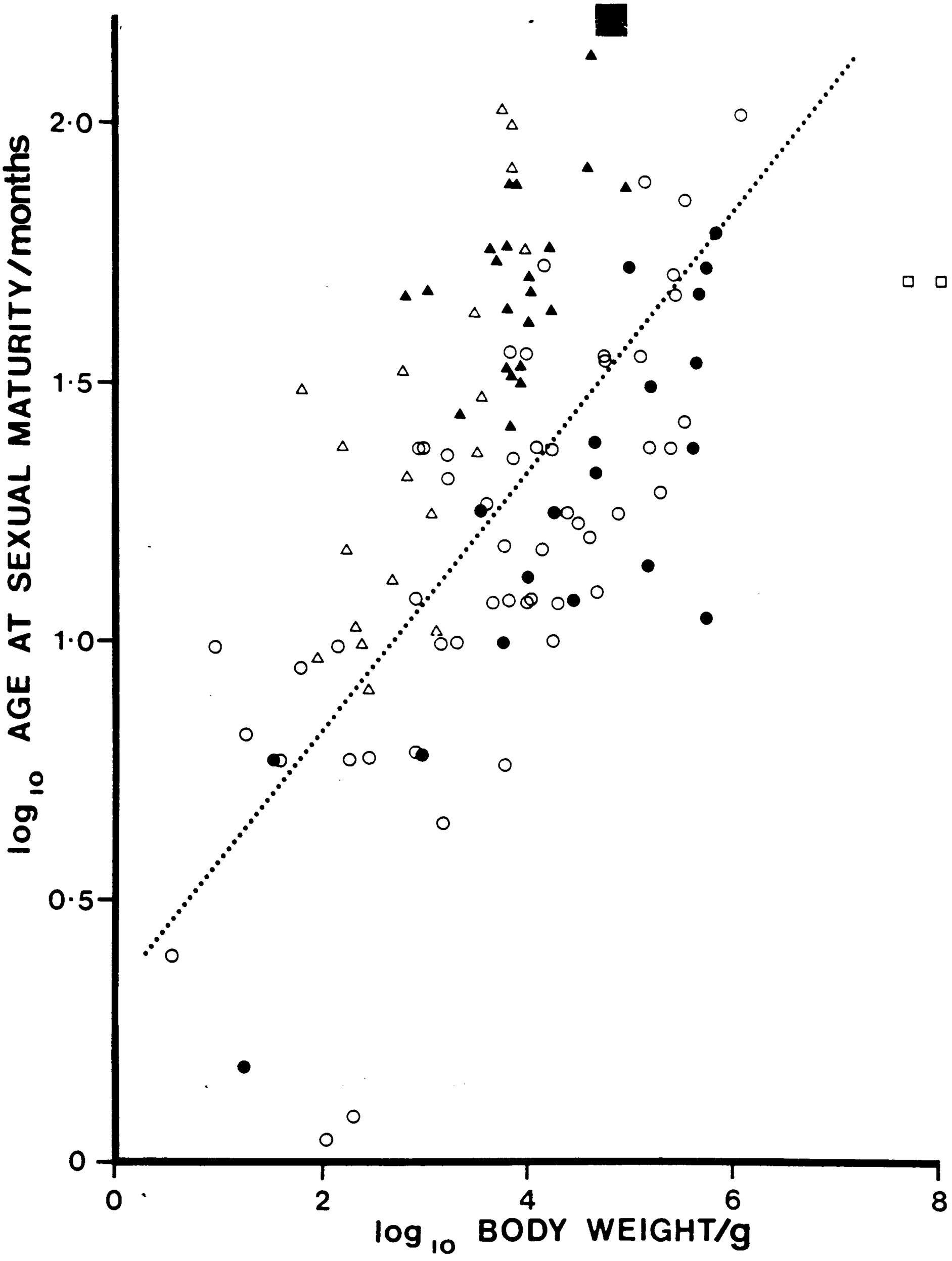


○ - MONOMORPHIC MAMMALS OTHER THAN PRIMATES
● - DIMORPHIC MAMMALS OTHER THAN PRIMATES
△ - MONOMORPHIC PRIMATES
▲ - DIMORPHIC PRIMATES
DOTTED LINE - MAJOR AXIS

Logarithmic plot of brain size against body weight for female mammals.

(After Willner & Martin, 1985)

FIGURE 3.2

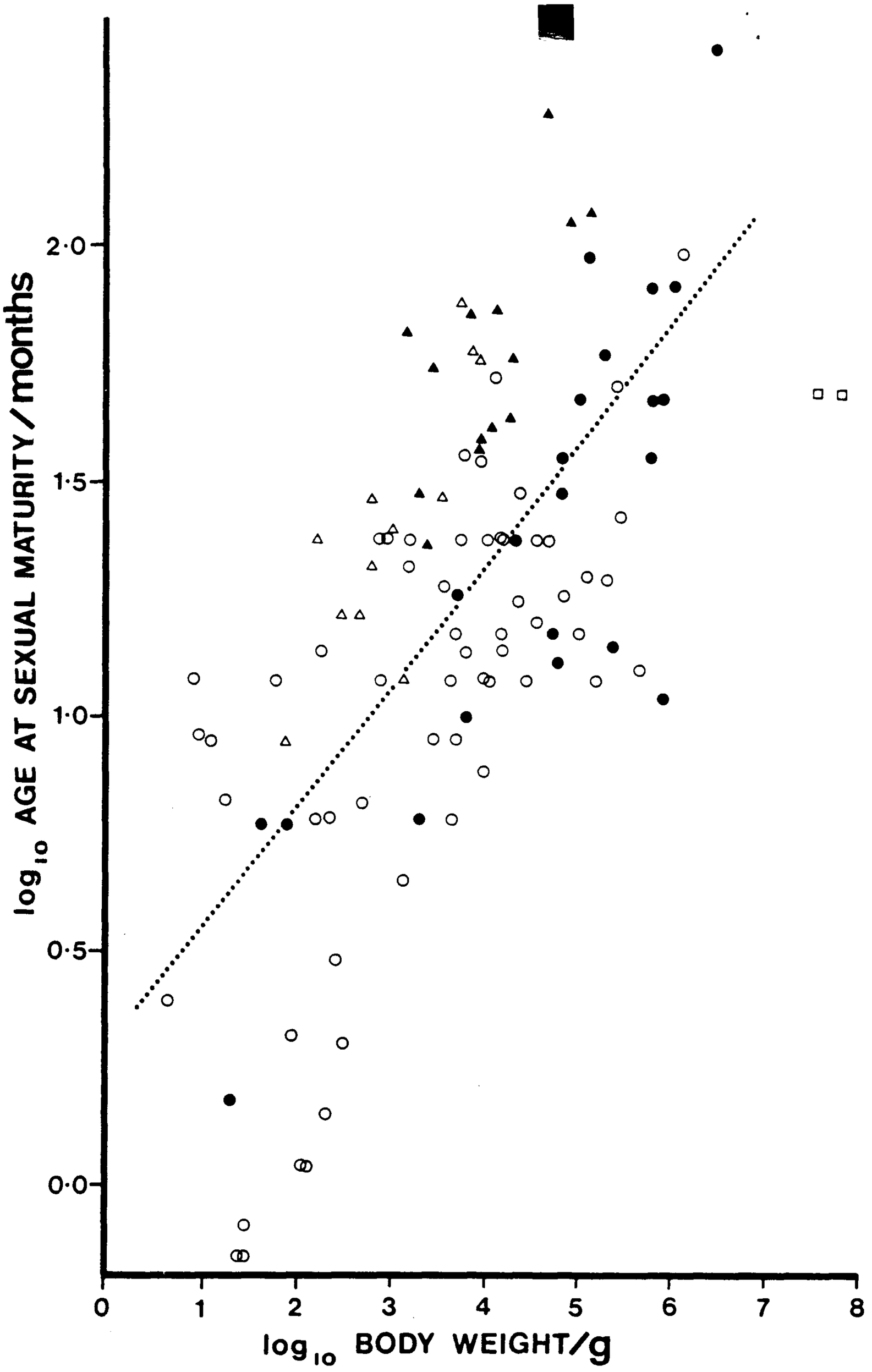


CONVENTIONS AS IN FIGURE 3.1 WITH ■ HOMO SAPIENS

□ CETACEANS

Logarithmic plot of age at sexual maturity against body weight for female mammals.

(After Willner & Martin, 1985)

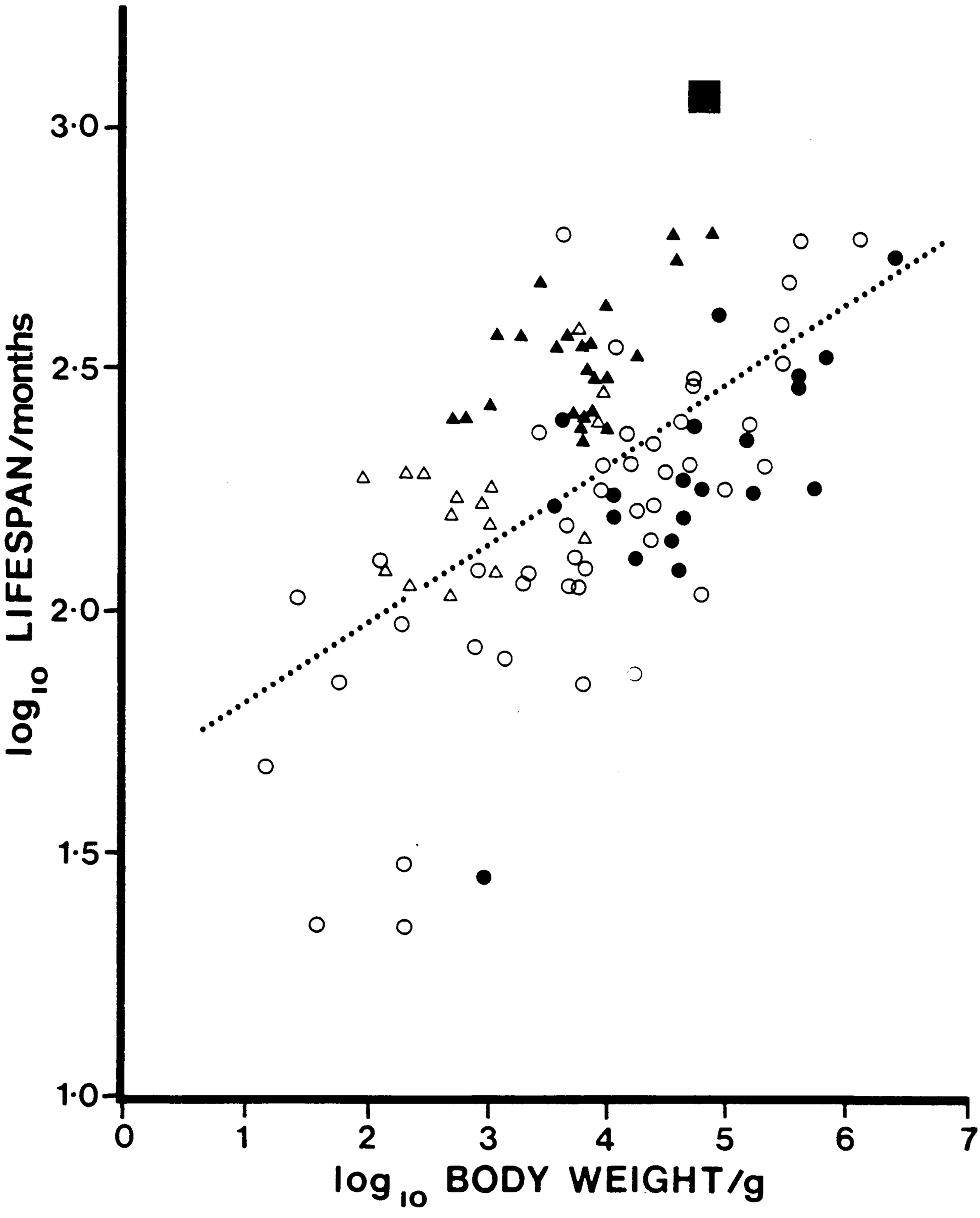


CONVENTIONS AS IN FIGURE 3.2

Logarithmic plot of age at sexual maturity against body weight for male mammals.

(After Willner & Martin, 1985)

FIGURE 3.4



CONVENTIONS AS IN FIGURE 3.2

Logarithmic plot of lifespan against body weight for female mammals.

(After Willner & Martin, 1985)

conception for females; use of age of potential rather than actual first breeding for males). Nevertheless, grade effects are clearly visible in the plots of age of attainment of sexual maturity against body weight, as can be seen for females in Figure 3.2 and males in Figure 3.3. Similarly, the bivariate relation between lifespan and body weight (Table 3.1) yields 68% unexplained variation for females and 59% unexplained variation in males. Again, although some of this variation is attributable to defects in the input data, such as difficulties in obtaining a realistic estimate of lifespan, the pattern which emerges indicates that grade distinctions are also involved (see Figure 3.4 for females).

Thus, major grade distinctions certainly seem to exist in the bivariate plots of age at sexual maturity and lifespan against body weight, while minor grade distinctions are evident in plots of brain weight against body weight. So it must be asked whether in these circumstances fitting a single line to the data is justifiable. Since primates clearly represent a fairly distinctive grade in having particularly late attainment of sexual maturity and particularly long lifespans at any given body size, possible grade distortion of the overall best-fit line can be tested by analysing primate and non-primate mammals separately and comparing the slopes

obtained for their respective major axes.

For the allometric relation between brain weight and body weight, the 95% confidence limits on the slopes of the major axes for non-primates (0.73-0.81 for females, 0.74-0.80 for males) contain the empirical slope values determined for primates alone (0.80 for females, 0.77 for males). Similarly, for the allometric relation between lifespan and body weight, the 95% confidence limits on the slopes of the major axes for non-primates (0.17-0.26 for females, 0.18-0.26 for males) contain the slope values determined for primates alone (0.21 for females and 0.23 for males). In the case of age at sexual maturity, the slope values for primates alone (0.32 for females, 0.30 for males) lie just outside the 95% confidence limits for non-primates (0.21-0.30 for females, 0.21-0.31 for males), but just within the 99% confidence limits (0.20-0.32 for females, 0.19-0.33 for males).

Consequently, grade effects can be said to have no significant influence on the slope of the overall best-fit line for either brain weight or lifespan. However, primates do appear to differ in respect of age at sexual maturity since they show somewhat higher slope values than other mammals. The difference, whilst small, is at a level which might be regarded as statistically significant. Even

so, the divergence is unlikely to affect the values of derived indices to a sufficient extent to modify the results discussed below. Hence it would seem justifiable to calculate logarithmic indices for males and females of individual species relative to the overall best-fit lines determined for all mammals taken together.

Table 3.1 also shows the results of allometric analyses involving pairs of variables without reference to body weight, namely for lifespan in relation to age at sexual maturity and for lifespan in relation to brain weight. Both of these instances yielded significant correlations, despite relatively high levels of unexplained residual variation. It therefore seemed appropriate to take these analyses further by examining the partial correlations between these variables remaining when other variables were controlled (Table 3.2).

It emerged that a highly significant relation between age at sexual maturity and brain weight remains when body weight and lifespan are controlled, either separately or together. On the other hand, partial correlations between lifespan and brain weight are generally lower when the other two variables (body weight; age at sexual maturity) are controlled. Indeed, when age at sexual maturity is controlled, either alone or in association with body

TABLE 3.2

RELATIONS BETWEEN LOGARITHMIC INDEX VALUES (ALL MAMMALS)

FEMALES

	n	r	r^2	p
Log IL vs. Log EQ	41	0.55	0.30	<0.0005
Log IL vs. Log IM	79	0.62	0.38	<0.0005
Log IM vs. Log EQ	36	0.81	0.66	<0.0005

MALES

	n	r	r^2	p
Log IL vs. Log EQ	44	0.62	0.38	<0.0005
Log IL vs. Log IM	63	0.59	0.35	<0.0005
Log IM vs. Log EQ	26	0.74	0.55	<0.0005

(Note: All logarithms to base 10)

(For definitions of terms see p.99)

weight, the correlation between lifespan and brain weight becomes insignificant (Table 3.3). This suggests that the association between lifespan and brain weight, which has been the source of so much discussion in the literature (Sacher, 1959, 1978; Cutler, 1975, 1976; Economos, 1980a, 1980b) may well be a secondary consequence of a primary linkage between age of attainment of sexual maturity and brain weight. Since, for all mammals, the age of attainment of sexual maturity is intimately associated with male and female reproductive strategies and directly relevant to the question of sexual dimorphism, such a finding highlights this particular variable as being especially significant.

In this context, it is worth considering directly one of the implications of the typical divergence in male and female growth trajectories associated with sexual dimorphism (see 4.3). It will be noted that in sexually dimorphic mammal species the larger-bodied sex (usually the male) typically attains a larger body size through a combination of more rapid growth and longer duration of growth prior to reaching the typical adult size for that sex. This suggests that in sexually dimorphic species there should be consistently later attainment of sexual maturity in the larger-bodied sex, whereas in monomorphic species ages at sexual maturity should be approximately

TABLE 3.3

PARTIAL CORRELATIONS FOR LOGARITHMIC VALUES OF AGE AT SEXUAL MATURITY, LIFESPAN AND BRAIN WEIGHT

AGE AT SEXUAL MATURITY VS. BRAIN WEIGHT

FEMALES

CONDITION	n	r(partial)	p-
Controlling for BODY WEIGHT	34	0.90	<0.001*
Controlling for Lifespan	34	0.63	<0.001*
Controlling for BODY WEIGHT AND LIFESPAN	33	0.83	<0.001*

MALES

CONDITION	n	r(partial)	P
Controlling for BODY WEIGHT	24	0.87	<0.001*
Controlling for Lifespan	24	0.61	<0.001*
Controlling for BODY WEIGHT AND LIFESPAN	23	0.86	<0.001*

Key: * = highly significant
(ns) = not significant

continued.....

LIFESPAN VS. BRAIN WEIGHT

FEMALES

CONDITION	n	r(partial)	p
Controlling for BODY WEIGHT	38	0.63	<0.001*
Controlling for AGE at SEXUAL MATURITY	34	0.16	0.17 (ns)
Controlling for AGE at SEXUAL MATURITY and BODY WEIGHT	33	0.15	0.20 (ns)

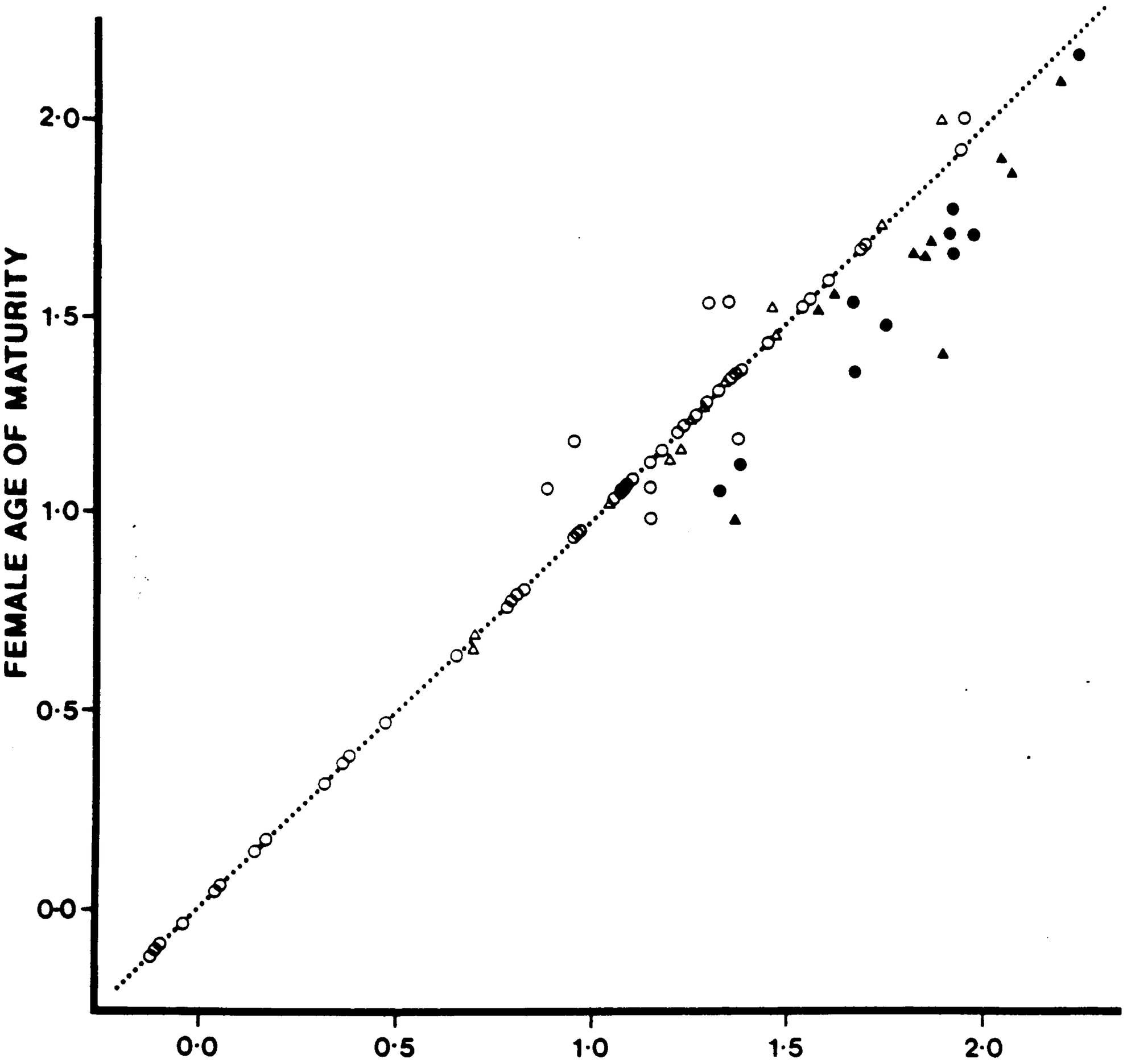
MALES

CONDITION	n	r(partial)	p
Controlling for BODY WEIGHT	40	0.37	<0.008*
Controlling for AGE at SEXUAL MATURITY	24	0.25	0.11 (ns)
Controlling for AGE at SEXUAL MATURITY and BODY WEIGHT	23	-0.23	0.14 (ns)

Key: * = highly significant
(ns) = not significant

the same for males and females. This can be checked by plotting female age at sexual maturity against male age at sexual maturity (Figure 3.5) and the prediction is very neatly confirmed. The plot clearly shows that in sexually dimorphic species (black symbols) females typically attain sexual maturity ahead of conspecific males. Accordingly, it can be concluded that - regardless of the direction in which selection may have operated (namely, either towards increased male body size or towards reduced female body size) - females of sexually dimorphic species tend (almost without exception) to breed earlier than the males. Nevertheless, the basic bivariate plots provide no clear evidence that earlier breeding in females is associated with any conventional grade distinctions between mammals and an explanation must be sought elsewhere. At this juncture the divergence between the levels of maternal investment prevalent among dimorphic and monomorphic simian primates (see page 145 et seq.) seem especially relevant.

Possible grade distinctions between dimorphic and monomorphic mammal species can also be examined by considering the logarithmic indices (see page 52) calculated on the basis of the original bivariate plots of brain size, age at sexual maturity and lifespan against body size. These indices are referred to as the



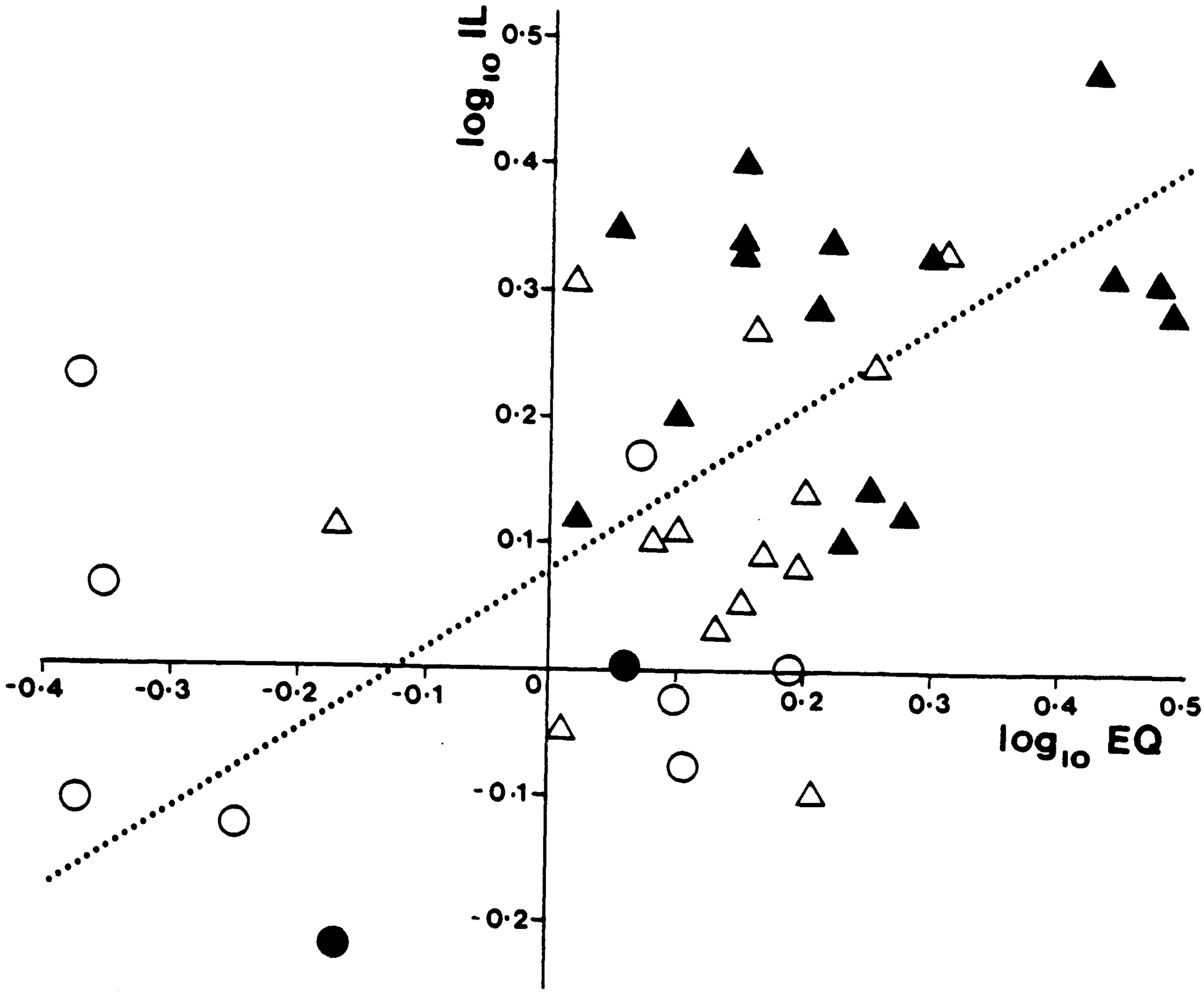
DOTTED LINE INDICATES EQUIVALENCE OF MALE AND FEMALE AGES OF SEXUAL MATURITY

CONVENTIONS AS IN FIGURE 3.1

Logarithmic plot of female age of attainment of sexual maturity against male age of maturity.

(After Willner & Martin, 1985)

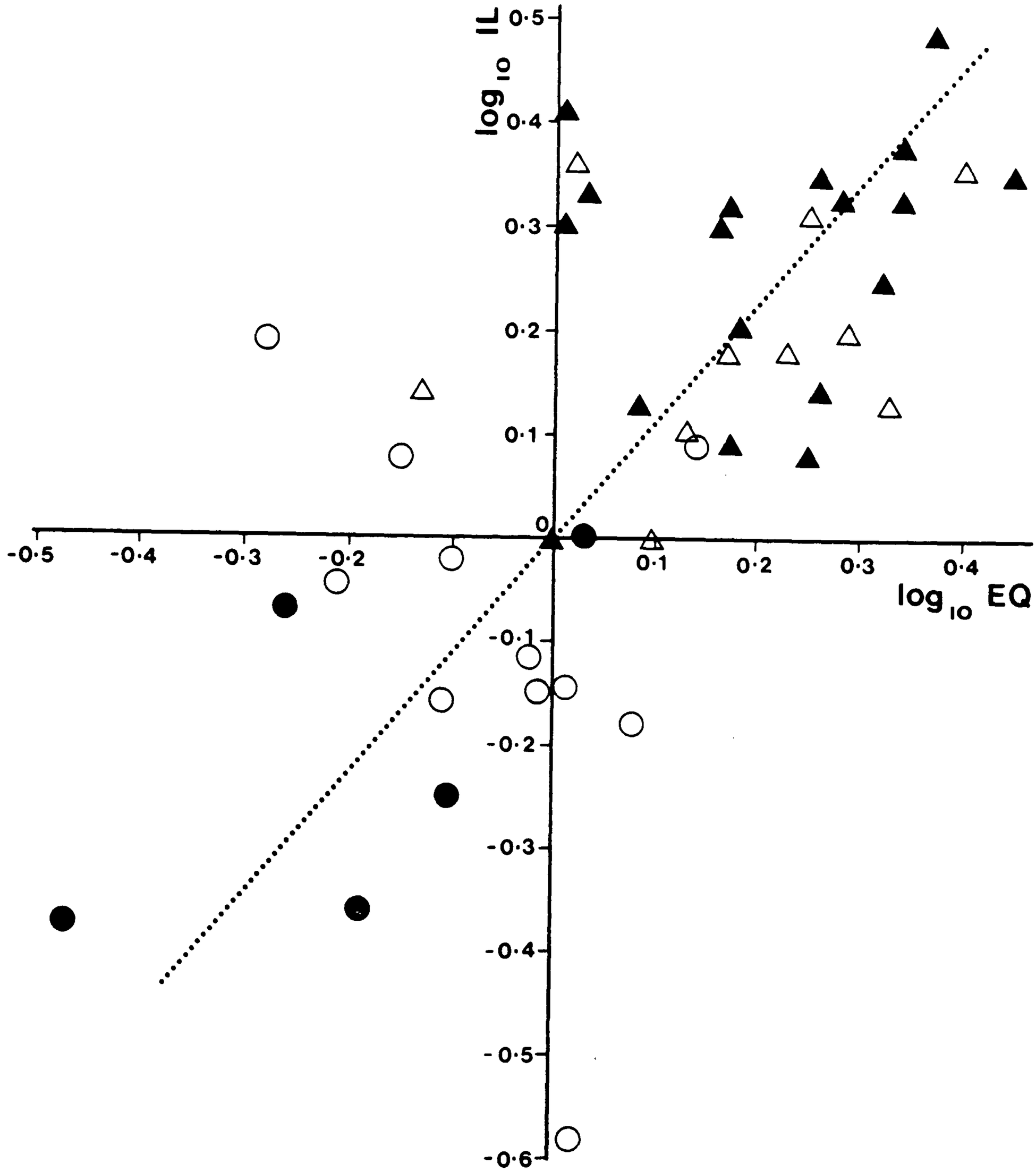
logarithmic encephalisation quotient (Log EQ), the logarithmic index of maturity (Log IM) and the logarithmic index of lifespan (Log IL), respectively. In principle, these indices have been freed of the influence of body size so that their implications can be considered in the absence of scaling effects. The index values have been analysed in pairs (Table 3.3, Figures 3.6-3.8) in order to identify their interactions and to seek differences between monomorphic and dimorphic species. It can be seen that all three indices (Log IL, Log IM, Log EQ) exhibit positive correlations when examined in this way. The index of lifespan and the index of sexual maturity are, for instance, quite strongly correlated, though there remains a fairly large proportion of unexplained variation (62% for females and 65% for males). The highest correlations are found in the relations between the index of sexual maturity and the index of encephalisation (Log IM versus Log EQ), with 34% unexplained variation for females and 45% for males. However, even if these results are taken to imply more than mere associations, and to reflect genuine interactions, none of the index plots shows any clear separation between dimorphic and monomorphic species. Thus, although allometric analysis (combined with the examination of partial correlations) has clarified a number of issues, most notably in identifying age of attainment of sexual maturity as a key paramter in various



CONVENTIONS AS IN FIGURE 3.1

Plot of logarithmic values of index of lifespan against logarithmic values of the encephalization quotient for female mammals.

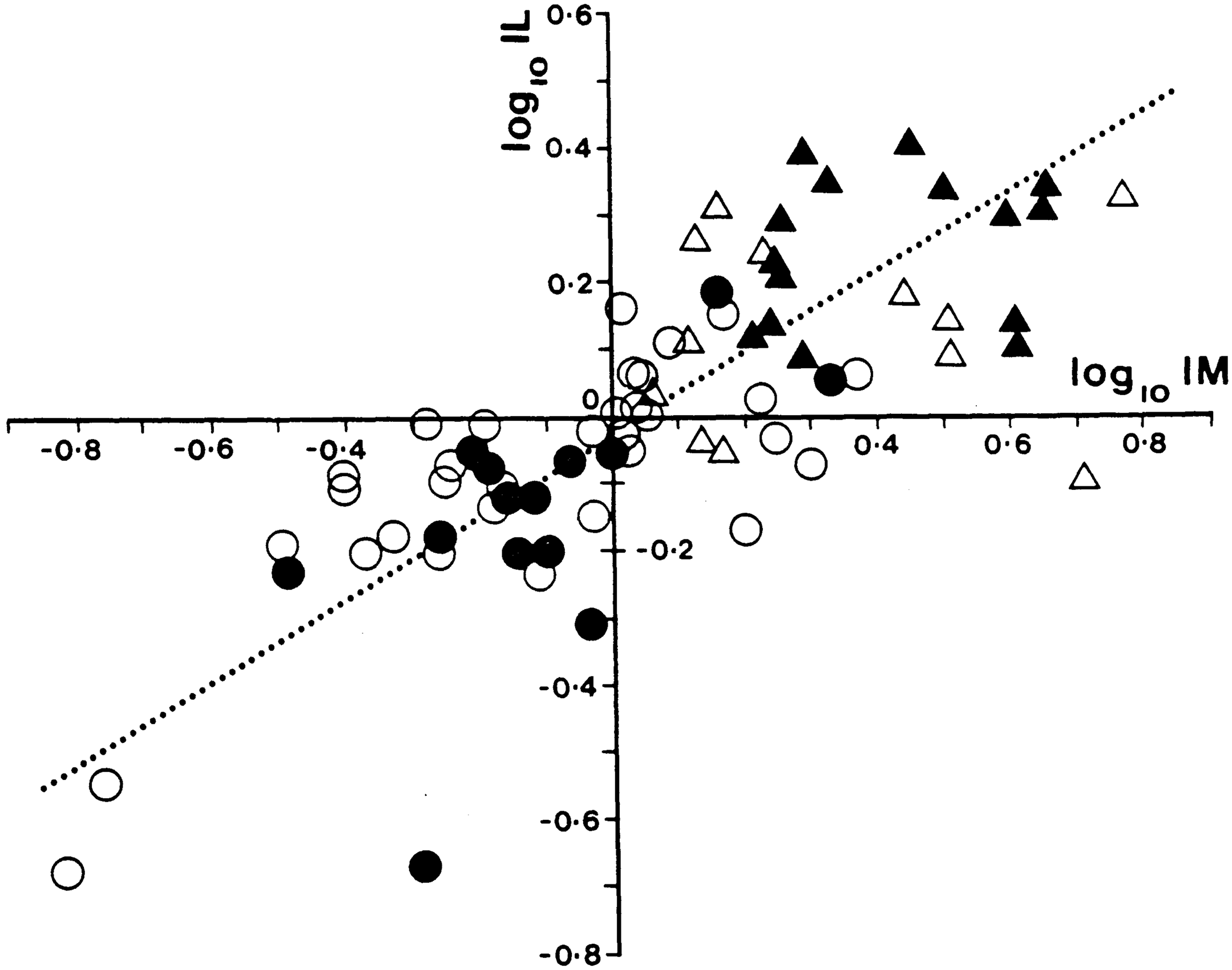
(After Willner & Martin, 1985)



CONVENTIONS AS IN FIGURE 3.1

Plot of logarithmic values of the index of lifespan against logarithmic values of the encephalization quotient for male mammals.

(After Willner & Martin, 1985)



CONVENTIONS AS IN FIGURE 3.1

Plot of logarithmic values of the index of lifespan against logarithmic values of the index of sexual maturity for female mammals.

respects, it has not revealed any general distinction between dimorphic and monomorphic species which might provide insights into the actual origins of sexual dimorphism.

At first sight, it might be expected that if sexual dimorphism relates to a shift in the age of attainment of sexual maturity in one or other sex, this should be disclosed at some stage of allometric analysis. In particular, females of monogamous, monomorphic species might be expected to exhibit some signs of delayed maturity (relative to body weight) as compared to females of polygynous, domorphic species. However, this expectation is frustrated by a circularity, relating to the suggested ontogeny of size dimorphism, from which it is difficult to escape. Let it be assumed, for instance, that the female of a dimorphic mammal species has achieved sexual maturity earlier in ontogeny relative to some monomorphic ancestral species. Since this results in both earlier breeding and a smaller adult female body size, the net result is that, on a bivariate plot, the point for that female is likely to move downwards along the best-fit line for mammals generally rather than away from it. In consequence, a plot of age of attainment of sexual maturity against body size is unlikely to reveal any grade distinction between monomorphic and dimorphic females.

Since phylogenetic size increase of males or size decrease in females must lead to virtually the same end results, it is extremely difficult to envisage some simple criterion which might separate these two evolutionary developments, or indeed, rule out the possibility that both male size increase and female size decrease have occurred.

Fortunately, special opportunities exist for breaching this circularity. These are provided by specific consideration of early maturing entities, such as the brain and molar teeth, in relation to overall body size. This line of enquiry is pursued for the brain in Chapter 5, in which findings of sexual dimorphism in the organisation of the brain are also appraised. Evidence stemming from an examination of molar tooth size is examined in Chapter 6 and reviewed in conjunction with the results obtained from the analyses of brain weights.

However, it is important to establish a solid foundation of observed facts relating to the ontogeny of sexual size dimorphism before engaging in further speculation as to its possible causes. The next chapter is dedicated to this end.

CHAPTER 4

ONTOGENETIC ASPECTS OF SEXUAL SIZE DIMORPHISM

4.1 OVERVIEW

The target size a mammal attains (Tanner, 1963) is the resultant of growth, maintenance and reproduction under constraint. Moreover, an animal that survives to full maturity must have achieved equilibrium within its surroundings at each intervening stage. In consequence, the implications of sexual size dimorphism are unlikely to be properly understood if attention is confined exclusively to the adult phase. It is imperative to examine the ontogeny of sexual size dimorphism since for males and females of the same species to differ in adult body weight, their respective growth patterns must have diverged at some postnatal stage if not already at birth. The factors which govern the emergence of sexual size dimorphism may reveal themselves by the developmental context in which their effects first become apparent. To this end, data relating to the onset of sexual size differences have been examined in the light of documentary evidence regarding the benefits and risks of differential growth rates.

An adaptively viable strategy calls for the continued survival of the adult mammal as a mature, sexually reproductive individual. This renders it difficult to

divorce the study of sexual size dimorphism from the more general problem of optimum body size; nor, perhaps, is it desirable to do so, since the distinction is really artificial. After all, sexual dimorphism in adult body size is merely the natural consequence of a difference in the optimum body size favoured for males and females of the same species under the joint constraints of a common phylogenetic and a divergent sexual inheritance. Moreover, once body weight has been ascribed a fundamental role in relation to survival, then monomorphic species become particularly interesting since for these the optima of both sexes apparently coincide. Perhaps it is significant that the same convergence occurs within dimorphic species throughout the period which precedes the initiation of differences in body size between males and females. However, in each of these instances the coincidence may be more apparent than real and need not represent either a common partitioning of resources or a similar total demand. Indeed, Trivers (1972) has cautioned that "even when ostensibly cooperating in a joint task male and female interests are seldom identical". This is scarcely surprising in view of the many factors differentiating male and female requirements as a direct consequence of primary sexual function. Yet it seems natural that differences in overall body size should barely be manifest between young males and females prior to puberty, whatever the ultimate divergence in their respective adult weights. At this early pre-reproductive stage they might be

expected to share the same risks and to experience their environment in much the same way.

Nevertheless, there are a few species for which the growth patterns of males and females have already diverged prenatally (see page 112). Yet, although minor differences in gestation period have been reported for male and female neonates of some of these species, it is still unclear whether differences between male and female birth weights reflect intersexual differences in duration or rate of prenatal growth. This remains a vital distinction in the postnatal ontogeny of sexual dimorphism in adult body size. Namely, whether it arises as a consequence of males growing faster or for longer than females of the same species. There is, moreover, no logical reason why both tendencies should not coexist and each of these options is examined in greater detail below (see 4.3).

However, whichever growth trajectory best accords with the available data - and there may well be a degree of interspecific variation - energy which is being channelled into growth is not available to sustain other activities, such as reproduction. Inevitably, there are benefits, costs and risks at stake in the allocation of limited resources; and whilst the larger, faster growing male may be better equipped to compete for scarce resources, his absolute requirements will have been increased and if he fails to meet these needs he will die.

The data suggest that once a strategy of accelerated growth has been embarked upon it cannot easily be reversed (see pp. 128-130) or modified. In view of the high mortality typically suffered by unweaned animals of both sexes, rapid early growth in males must offer a major selective advantage in later years to warrant this additional hazard (see pages 128-130). In contrast, if females sacrifice growth potential to more rapid sexual maturation, how disadvantaged are they in comparison with the larger, stronger males in obtaining the resources necessary for their survival?

The importance of size as a determinant of survival (see 1.2) has already been discussed. In its turn, the energy an animal can acquire and utilise is the most immediate determinant of its size through each developmental phase and takes on a special significance in the case of birds and mammals, which are unique in exhibiting a target size (Tanner, 1963). It may safely be assumed that this size represents a stable system within an environment which affords the mature individual sufficient resources to generate the energy needed for maintenance and reproduction, but only in the absence of further growth. Thus, in order to understand the factors which govern the ontogeny of sexual size dimorphism, it is necessary to examine the sources of energy available to the growing mammal, male or female, from conception through to adulthood. There are four recognisable phases: prenatal,

when dependence on maternal investment is complete; postnatal, but prior to weaning, with maternal investment still the primary source; post-weaning, but possibly still with some parental investment in the form of defence and continued occupation of parental territory; full independent adulthood, when further cooperation between individuals, in the context of kin selection or other forms of coalition, is likely to entail a degree of reciprocal investment typically absent from the interactions between parents or other relatives and immature animals.

There are two separate, though related, questions to be considered in relation to the ontogeny of sexual size dimorphism. Firstly, individuals which attain the same adult body weight need not necessarily have shared a common growth trajectory; in addition, for those species which do show sexual size dimorphism between adult males and females, it is important to determine the developmental phase at which the divergence initially became apparent as well as to monitor its subsequent intensification. Secondly, it is quite conceivable that males and females, as they progress towards their respective target sizes will, by virtue of physiological differences, and irrespective of differences in growth rate or absolute body size, have different energetic requirements. An appreciation of these needs and an understanding of the strategies adopted to meet them are

both dependent upon a firm basis of factual information on size and growth.

In the attempt to acquire a sound data base many published sources were carefully sifted (see Appendix 2.2). The problems typically associated with the use of secondary data were frequently encountered, especially in the context of field studies. There was often insufficient detail relating to sex, age and sample size; a common weight for young and immature animals of both sexes had often been assumed, so that average species weights alone were presented, with no breakdown by sex. To counteract these difficulties some previously unpublished material was specifically sought out, with the generous cooperation of several individuals. In addition, a personal search was carried out on the records of a captive colony of crab-eating macaques, Macaca fascicularis, maintained by the Royal College of Surgeons of England. This exercise yielded useful results as well as highlighting the problems of obtaining data for a consistently large sample. Some monkeys died, or were removed from the colony for other reasons; others were introduced as infants or juveniles. A great asset was that all the animals had been bred in captivity and their ages were accurately known. However, although the monkeys were frequently weighed, this was not done at regular intervals, but according to when other observations were to be made - the colony is maintained for purposes of dental research. Since

weighings were usually carried out every two or three weeks (even daily for infants) it was assumed that linear interpolation would yield sufficiently accurate data for use in the estimation of average weights at specific ages. A computer program was written to convert the raw data into mean weights for male and female macaques, at weekly intervals, from birth through to adulthood. Sample sizes ranged from 12 males and 11 females at one week old, through 24 males and 28 females at nine months to 12 males and 13 females at two years. From three years, the sample sizes declined from 6 males and 7 females to only 2 or 3 of each. At every age, data relating to animals that were reported as sick were omitted.

Empirical data are presented below to illustrate the growth patterns of both monomorphic and dimorphic species. These are then examined in the light of data relating to survival and the resources available from conception to full adult maturity. Maternal investment is assigned a major role, both prenatally and during early development, and is discussed in some detail (see 4.4).

4.2 BIRTH WEIGHTS

There are essentially two questions relating to the possibility of sexual size dimorphism at birth; namely, whether differential prenatal development of males and females is theoretically attainable and, if so, whether such weight difference by sex would be likely to confer

any selective advantage on the neonate (of either one sex or both). Considering first the feasibility of intersexual birth weight dimorphism, this could presumably be determined via the placenta. Although maternal recognition of the sex of the offspring *in utero* might conceivably present difficulties for such a mechanism, the problem would not seem to be insurmountable. For instance, an excess of threats and attacks directed at mothers pregnant with females in comparison with those carrying males has been noted for both pigtail and rhesus macaques (Simpson *et al.*, 1981). These results corroborate those of Sackett *et al.* (1975), in their earlier study of captive *Macaca nemestrina*. In the course of this study it was also reported that the discrimination occurred only during the latter half of pregnancy, when fetal hormones circulating in the mother's blood were presumably communicating information as to its sex. Since it appears that other group members can recognise the sex of the unborn infant, it would be highly unlikely for the mother herself to be incapable of the same degree of discrimination. Furthermore, Clutton-Brock and Albon (1982) report that, for red deer, male calves have significantly longer gestation periods and heavier birth weights compared with females, whilst among elephant seals and patas monkeys males are not only born heavier but also immediately grow faster than females (elephant seals: Reiter *et al.*, 1978; patas monkeys: Sly *et al.*, 1978). There consequently seems no reason to doubt the possible

existence of a mechanism capable of promoting sexual size dimorphism at birth.

On the other hand, there might equally well be a maternally-oriented argument for the relative absence of intersexual differences in neonatal body weight, especially with respect to an upper limit on size. Selection could favour a single optimum birth weight relative to the mother's resources during both pregnancy and lactation (Robbins and Robbins, 1979 and pages 143-144), with a further limitation imposed, at least in some cases, by the dimensions of her pelvic canal. On this basis, if intersexual weight differences were already advantageous at birth, these might be expected to occur at least in species for which the female is larger than the male and for which, as well as a relaxation in other maternal constraints, parturition difficulties need not restrict an increase in the birth weight of the larger sex. So far, the available data, which are unfortunately rather limited, show no evidence of such an effect. Data for cetaceans (Lockyer, 1977), in which there is no pelvic constraint on neonate size, indicate equal birth weights for both sexes in species for which the female is the larger adult. Taken overall, in so far as the optimum birth weight favoured for either sex relates to the mother's interests, energetic constraints are likely to be of prime importance. It is unlikely that the dimensions of the pelvic canal impose a limit on the size of the fetus

in most mammals; humans seem to be relatively exceptional in this respect. In addition, since neonatal weight is related to maternal weight in a negatively allometric fashion, the probability that neonatal size is limited by the birth canal should decrease with increasing maternal weight. This is especially relevant as it is typically the larger species within a taxon which exhibit a high degree of body size dimorphism, including such extreme examples as whales, elephants and gorillas.

However, it is quite likely that body size dimorphism between male and female neonates frequently goes undetected. Very large samples are required to establish the statistical significance of differences of small absolute magnitude, especially between variables which are subject to high levels of variation, such as birth weight. After all, sexual dimorphism in human birth weights was only demonstrated during the course of observations on all births (23,970) in Birmingham for an entire year (Gibson and McKeown, 1952). Such extremely large sample sizes are generally restricted to epidemiological studies and are not normally available for either non-human primates or for other mammals. A more recent study carried out on 106 term infants of each sex during the first 48 hours of life in two Liverpool maternity hospitals indicated an overall reduction in 32 body dimensions in females compared with males. Significant differences were found for head circumference, head length and upper leg length, with the

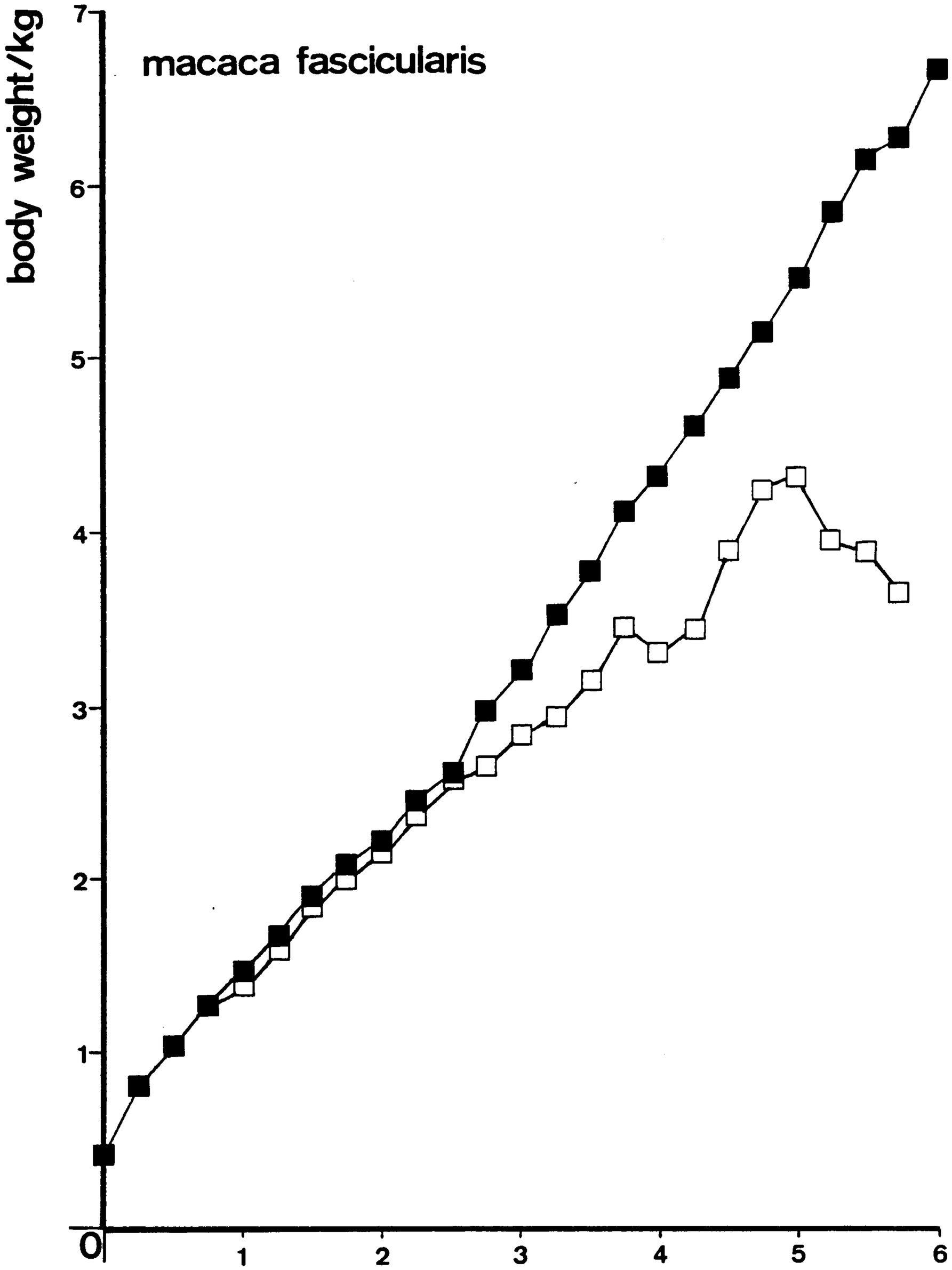
other parameters just failing to reach statistical significance (Dangerfield and Taylor, 1983). Although even the significant differences were relatively mild, it seems unlikely that such a broad spectrum of intersexual differences would have arisen entirely at random. The biological importance of this early divergence may be that, though small in absolute terms, it reflects the prenatal establishment of male and female growth trends that will ultimately govern the long term development of the neonate according to its sexually appropriate target size.

There may be an additional factor governing the very minor scale and limited occurrence of intersexual differences in birth weight. As well as maternal limitations, it may not be feasible for male neonates to be much larger and heavier than females on account of subsequent problems in obtaining the essential resources for growth and maintenance at an increased weight for age (see pages 128-129). At the same time, even when targeted towards a smaller adult body size than conspecific males, a young female may be critically disadvantaged if she is much smaller than the males within her age cohort, since she will be in competition with these animals during her early developmental period. Moreover, in view of the association between birth weight and survival which has been noted for humans (Frisch, 1972) and is probably also valid for primates and other mammals, there would seem to

be no reason for female neonates to be smaller or lighter than absolutely necessary in accordance with maternal constraints and subsequent nutritional needs as independent juveniles.

A survey of the literature shows that, as a general rule in mammals, intersexual body size differences between infants and young, immature animals tend to be small, even for species which show a marked degree of sexual size dimorphism between adults. The first really pronounced divergence in male and female body weights usually coincides with the onset of puberty (see Figures 4.1, 4.3 and pages 124-125), confirming that there is generally little or no positive selection for sexual size difference at birth. Data from a sample of mammal species (Table 4.1) illustrate this common trend.

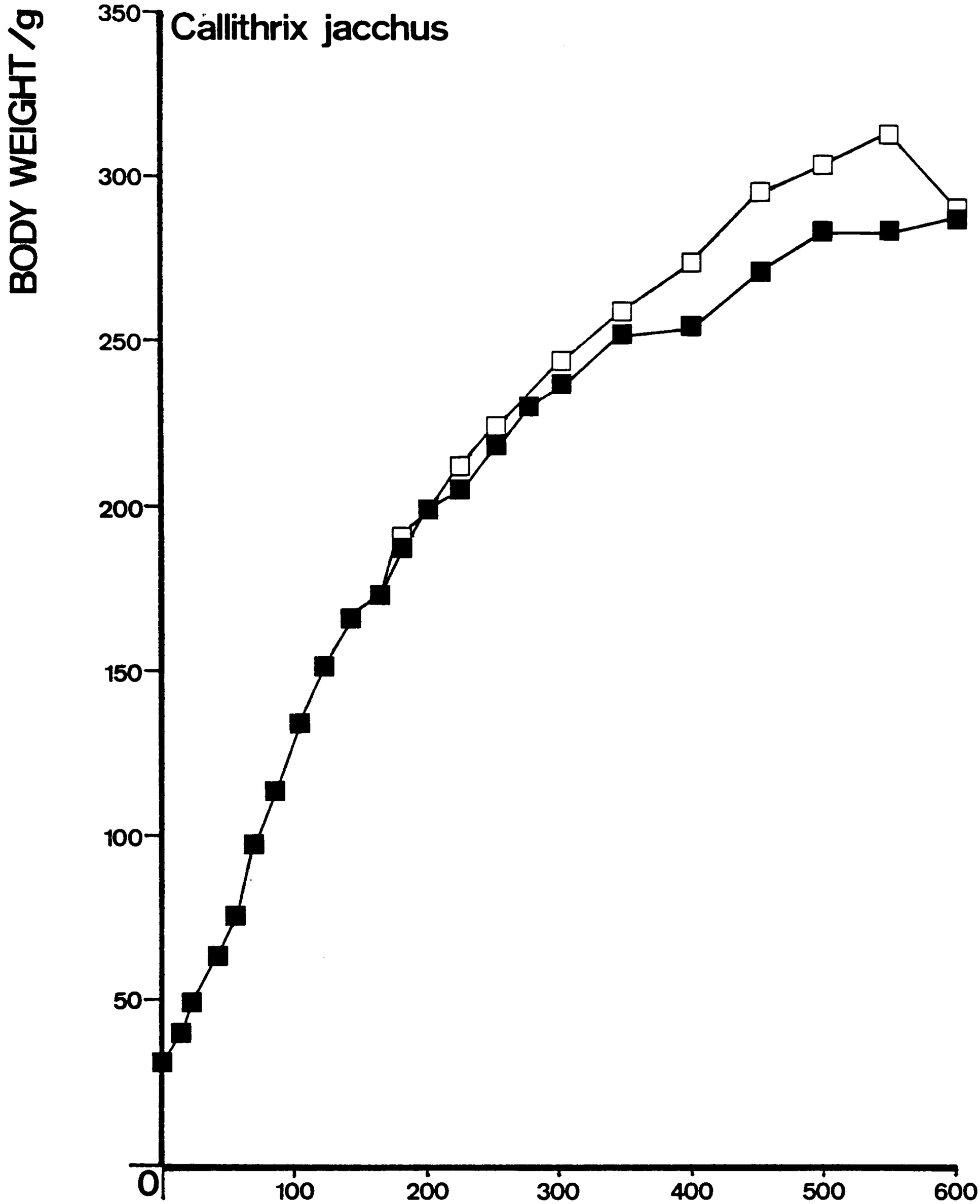
Yet the typical absence of pronounced intersexual size differences at birth may mask complexities in both the prenatal and postnatal allocation of maternal resources between male and female offspring. Differences in maturity are not necessarily reflected in differences in body weight (see page 140), which may help to explain such anomalous contrasts as the longer interbirth interval reported among red deer and elephants after delivery of a male calf (deer: Clutton-Brock et al., 1981; elephants: Lee & Moss, 1986) and the unexpectedly shorter interval that follows the birth of a male rhesus monkey, although



□ FEMALE ■ MALE

Growth curves for male and female crab-eating macaques

(After Willner & Martin, 1985)



□ FEMALE ■ MALE

Growth curves for male and female common marmosets.

(DATA FROM LUNN, 1981)

(After Willner & Martin, 1985)

TABLE 4.1

RATIOS OF MALE TO FEMALE WEIGHTS AT BIRTH

(Figures in brackets denote adult weight ratios)

ARTIODACTYLS	
Cattle	
Ayrshire	1.03 (1.08)*
Guernsey	1.09
Holstein	1.14 (1.55)
Jersey	1.08 (1.00)
Cervids	
Barren ground carribou (*Rangifer tarandus tarandus*)	1.10 (1.48)
Red deer (*Cervus elaphus*)	1.08
Goats	
Angora	1.10 (1.90)
Saanen	1.14 (1.09)
Toggenburg	1.13 (1.23)
CARNIVORES	
Cat	
Domestic cat	0.94 (1.31)
Dogs	
Beagle	1.03
Cocker spaniel	1.00
Shetland sheepdog	1.05
RODENTS	
Mouse (piebald)	0.99 (0.97)*
Rat (Wistar)	1.06 (1.50)*
Guinea pig	1.06 (0.95)*
PRIMATES	
Callithrix jacchus	0.98 (1.01)
Erythrocebus patas	1.16 (1.99)
Macaca cyclopsis	1.02
Macaca fascicularis	0.98 (1.52)
Macaca mulatta	1.04 (1.17)
Macaca radiata	1.06
Homo sapiens	1.04 (1.08)

* denotes weight ratio at 12 months

several studies have shown that, like red deer and elephants, male rhesus neonates tend to be slightly heavier than females (Simpson et al., 1981). Since infant mammals are entirely dependent on their mothers, the postponement of a subsequent pregnancy is likely to have an indirect bearing on postnatal survival chances. However, growth and ontogeny are continuous processes, so that a fuller discussion of the availability and allocation of maternal resources has been deferred (see 4.4) pending a review of those data which enable the bare facts of sexual size dimorphism to be presented at successive developmental stages.

4.3 THE POSTNATAL ONTOGENY OF ADULT SEXUAL SIZE DIMORPHISM

It has already been suggested that, prior to puberty, constraints on body size and growth rate are likely to be very much the same for both males and females of a single species (see pages 106-107). Unweaned and immature animals are probably the most vulnerable so that, even if extreme sexual dimorphism is ultimately attained between adults, it may not be possible for it to be developed early in life; the energetic costs and risks to the faster growing sex might simply be too great. On this basis, a common growth trajectory might reasonably be expected during infancy and the early juvenile period even for mammal species which are highly dimorphic when fully grown. However, as some species already exhibit minor differences in body weight between male and female

neonates, this general expectation needs either to be confirmed or refuted. At the same time, differences in the energy input required to initiate and maintain intersexual differences in growth rate, either prenatally or during early development, might imply that the sex of the infant acts as a mediator for the level of maternal investment. At this early stage in mammalian life history, the mother is virtually the only source of nourishment. But it has yet to be established that the energetic needs of infant males and females are determined solely by their respective body sizes and growth rates; intersexual differences in activity patterns could also influence the total need for resources. Nevertheless, a clear picture of what is actually happening, in terms of male and female growth trajectories, is an essential precursor to more general considerations of possible intersexual differences in the overall demand for energy.

Even for those species with an element of sexual size dimorphism already apparent at birth, the magnitude of this intersexual weight difference is trivial compared to the difference in body weight between fully mature males and females. Thus, for patas monkeys, although the intersexual body weight difference is already statistically significant at birth ($p < 0.01$; Sly et al., 1978), the neonatal male:female body weight ratio is only 1.16 compared with an adult male:female ratio of 1.99 (data of present study). It seems that the major impetus

towards adult size dimorphism occurs postnatally and, before trying to evaluate possible differences in the levels of maternal investment accorded to sons and daughters, it is necessary to establish whether the divergence between male and female growth trajectories occurs prior to weaning. Thereafter, regardless of the timing and whether it follows a period of monomorphism or of slight intersexual weight difference, the full expression of adult size dimorphism could be attained by subsequent more rapid growth in the larger sex or longer duration of growth in the larger sex or a combination of both of these.

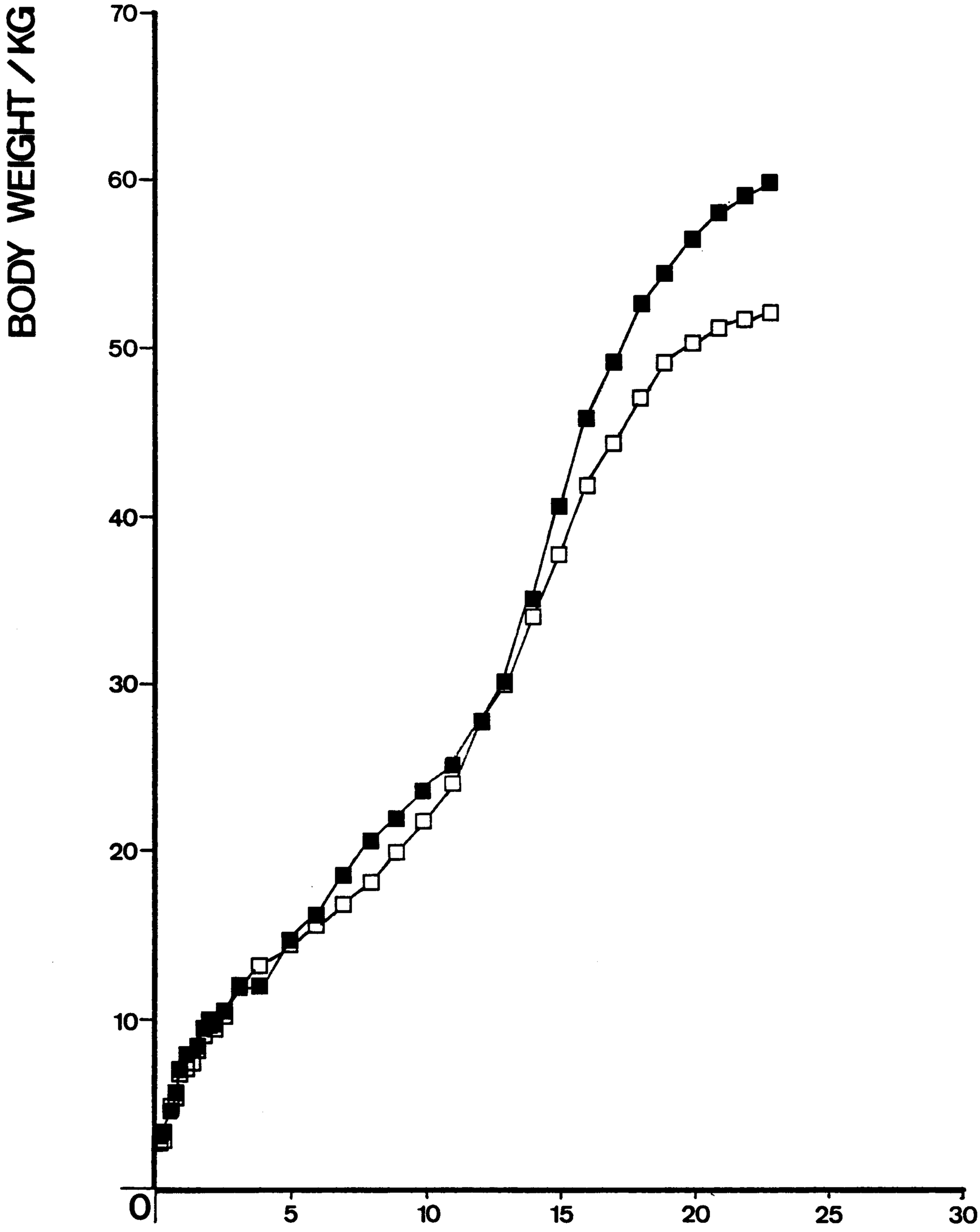
A choice must be made between the three alternatives, since otherwise it will not be possible to probe either the diverse energetic requirements of males and females or the life history strategies adopted in response. The extent to which each of the suggested growth patterns accords with currently available data is the sole arbiter between them and could well vary even between species that show the same degree of body size dimorphism between fully mature adults. Moreover, analysis of these same data might serve to uncover those features, if any, which distinguish between monomorphic, mildly dimorphic and strongly dimorphic species. Although the weight data presented below mostly stem from captive bred or domestic species they are probably the most suitable, since accurate ageing of wild caught individuals is seldom feasible. The aim has

been initially to describe the visible, external features in the ontogeny of sexual size dimorphism and then to use this information as the basis for an enquiry into the energetic needs and life history strategies that underly the observable facts.

Georgiadis (1985) compared the body-weight growth curves for males and females of eleven uniparous African ruminant species, ranging in mature size from 20 to 600 kg. and concluded that: "Male and female growth patterns differ in several ways. Males of sexually dimorphic species attain a mature weight that is greater than that of females by growing slightly faster than females and more importantly, by continuing to grow after female growth has stopped". Examination of the detailed data available for crab-eating macaques, Macaca fascicularis (personal observation, see page 110 and Figure 4.1), and marmosets, Callithrix jacchus (Figure 4.2, based on data from Lunn, 1981), indicates that for both these species size differences between infants and juveniles tend to be insignificant and are probably, for the most part, attributable to sampling variability. The marmosets subsequently remain monomorphic into adulthood whereas the macaques show quite pronounced sexual dimorphism as adults. Figure 4.1 illustrates the continued growth of the male macaque for some years after the female has attained adult body weight. Moreover, data from Spiegel (1956) indicate that the growth curve for castrated male

crab-eating macaques is intermediate between those for intact males and females. A sequence of average body weights for human males and females, spanning the period from birth to maturity (Vierordt, 1890; Figure 4.3) further corroborates the relative absence of intersexual weight differences prior to puberty. It is noticeable that even in this moderately dimorphic species, male growth continues beyond the age at which the females have achieved full adult weight .

In the course of an extensive analysis covering eighty five measurements taken on a sample of one hundred and thirty one gorilla skulls of different dental ages, Stratil and Schmid (1984) concluded that "sexual dimorphism remains insignificant until the last stage of ontogeny is reached". Another enquiry, carried out at the Jersey Zoological Park, monitored the physical development of 6 hand-reared lowland gorilla infants, 4 males and 3 females, from birth to twelve months. There was no indication of body weight divergence along sexual lines prior to one year, the oldest age for which data were available (Usher-Smith et al., 1976). This convergence is particularly striking since adult male gorillas weigh twice as much as adult females. Several other studies have yielded comparable findings during both infancy and subsequent development for a variety of primate species (Dixson, 1981; Froehlich et al., 1981; Gautier-Hion and Gautier, 1985; Gavan, 1953; Grether and Yerkes, 1940;

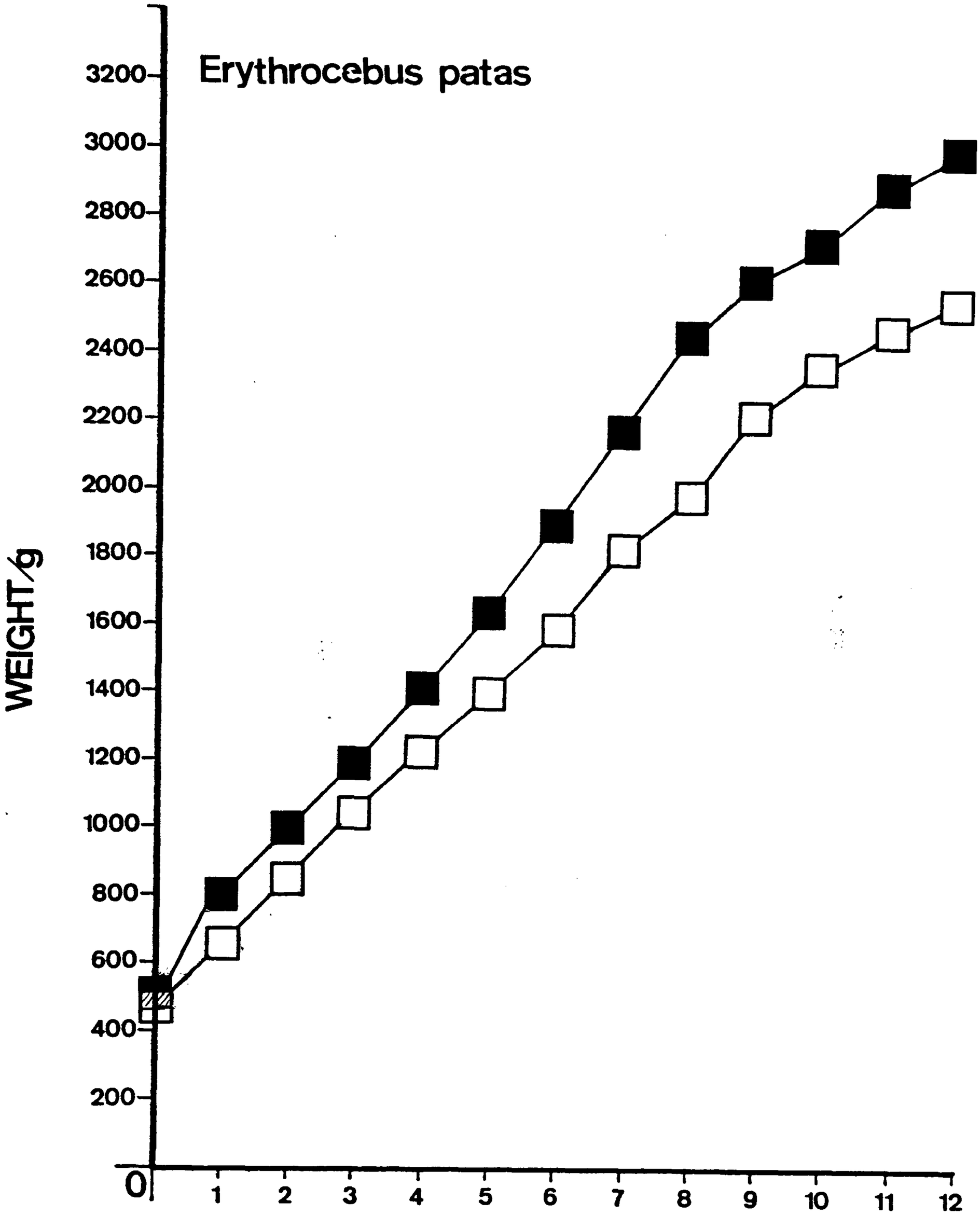


Growth curves for male and female Homo sapiens.

(DATA FROM VIERORDT, 1890)

H. Kummer, pers. comm.; Shea, 1983; Spiegel, 1956). Consistently similar developmental patterns are also indicated for several non-primate mammals (Dik dik: Kellas, 1955; Elephant: Laws, 1966; Cetaceans: Lockyer, 1977).

Nevertheless, there do seem to be some deviations from the general trend regarding both birth weights and early growth rates and it may be possible to draw useful inferences from the distribution of these exceptions. In particular, it is notable that they appear to be confined to relatively large species and are most pronounced in those which ultimately attain a high degree of sexual size dimorphism. Male patas monkeys are already slightly but significantly heavier than females at birth (Sly et al., 1978) and this divergence increases throughout ontogeny. Despite the variability within the rather small sample (13 males and 18 females from birth to 6 months, 8 males and 7 females subsequently), the consistency of the greater male body weight in comparison to that of the female is quite striking (Figure 4.4) and attains a high level of significance, (Sign test; $p < 0.001$, based on data from Sly et al., 1978). In contrast, extensive overlap was found between the weight ranges of 37 male and 29 female chimpanzees, all captive born and maintained in the same colony. Moreover, during the first nine years of life, as the variability in weight gradually increased for both sexes, the largest females were heavier than the largest



SAMPLE SIZES:	MALE	FEMALE
BIRTH TO 6 MONTHS	13	18
6 MONTHS TO 1 YEAR	8	7

Growth and development of patas monkey.

(DATA FROM SLY ET AL., 1978)

males and the smallest males were lighter than the smallest females, both being matched for age. By about twelve years the female distribution had levelled off whereas the male distribution still appeared to be increasing (Gavan, 1953).

It is appropriate to consider the costs and risks associated with this early divergence, which is conspicuously absent from the developmental patterns of monomorphic species such as Callithrix jacchus and howler monkeys (Froehlich et al., 1981). In contrast, the barely realised tendency for males of strongly dimorphic species to be systematically somewhat larger than their female counterparts suggests the existence of a powerful drive towards more rapid growth in these males, immediately from birth; yet this seems to be inhibited, or held in check, by some other and equally powerful constraint. The counterforce could well be the threat to survival entailed in premature rapid growth, an explanation which is in harmony with observations of differential mortality between male and female infants and juveniles in such species. Indeed, the potential costs of accelerated growth are well illustrated by Drickamer's observations of free ranging rhesus macaques. Both sexes survived in equal proportions until four years. Males subsequently incurred a higher mortality rate whilst that for females remained constant and very low (Drickamer, 1974).

It is unlikely that this synchrony between the increase in male mortality and the increase in male growth rate that also typically occurs at about four years of age should be a chance coincidence. Clutton-Brock et al. (1985) consider that "the distribution of mortality in red deer and other mammals suggests that higher mortality rates among male juveniles are a consequence of a greater susceptibility of males to food shortage associated with their faster growth rates and increased nutritional requirements". The African elephant affords a further corroborative example; males are already slightly heavier at birth and then immediately grow more rapidly than females, even in infancy. During drought years these immature males suffer a much higher mortality rate than females of the same age (Lee & Moss, 1986) and this may be linked, at least circumstantially, with the extent to which the rapid growth rate of the young male, from birth onwards, not only dramatically outstrips that of the female, but also possibly leads him to exceed the optimum size for survival under adverse climatic conditions. "During wet years there was little difference between sexes in survivorship", but under situations of reduced food availability mothers were apparently "unable to sustain milk production at a level that met the metabolic needs of their sons, and as a result male calves were more likely to die" (Lee & Moss, op. cit.).

It seems that for certain species the high premium associated with large body size in adult males exposes infant and immature males to high levels of risk which reduce the probability that they will survive into adulthood. However, although in these instances the premature rapid growth of young males certainly makes a major contribution to their greater mortality in comparison with females, it would be an over-simplification to regard this as the sole cause; too many anomalies would be left unexplained. As cited by Clutton-Brock et al. (1985) "these include a small but consistent tendency for males to show a higher hatching or neonatal mortality in some species showing little size dimorphism (including thoroughbred horses and man): the absence of evidence that the direction of differential mortality is reversed in species where females are larger than males.....: and the tendency for male fetuses to be less viable than females during the early stages of gestation".

Postnatally, differences in the social environment experienced by subadult males and females could also make a substantial contribution to intersexual differences in mortality. For instance, following their study of the demography of howler monkeys, Alouatta palliata, Froehlich et al. (1981) concluded that increased mortality among subadult males was due to inadequate diet "ultimately caused or potentiated by adult male

aggression". In contrast, Dittus (1977) found that juvenile females suffered the highest mortality when a population of toque macaques experienced an acute food shortage. He attributed this to the inability of these young females to attract support from other animals in the form of coalitions. They were consequently less able to defend themselves and successfully compete for limited resources. Thus, juvenile mortality may show a distinct sex bias. It is also liable to vary within sex, according to maternal status. Both tendencies are exhibited by savannah baboons, Papio cynocephalus. The probability of survival to maturity is greater for daughters of high-ranking baboon mothers than for either their sons or the daughters of low-ranking females. In addition, the sons of low status mothers are not only more likely to survive than their daughters, but also have a better chance of reaching maturity than the sons of high-ranking females (Altmann et al., 1986). Similar juvenile mortality patterns were found among bonnet macaques, except that for this species survival rates were high for infants of either sex born to high ranking mothers.

These important studies demonstrate uneqivocally that mortality is not evenly distributed between the various age-sex classes. Sex and status will consequently constrain the tactics an individual must adopt in order to survive. Dunbar (1988) cited four main causes of mortality: starvation, disease, temperature stress and

predation. However, it is unlikely that even mature adult body weight, much less growth rate, is simply related to any of these factors. Nevertheless, the link between size and survival attests to some form of relationship and strategies to avoid premature death presumably have a profound effect on both rate and duration of growth.

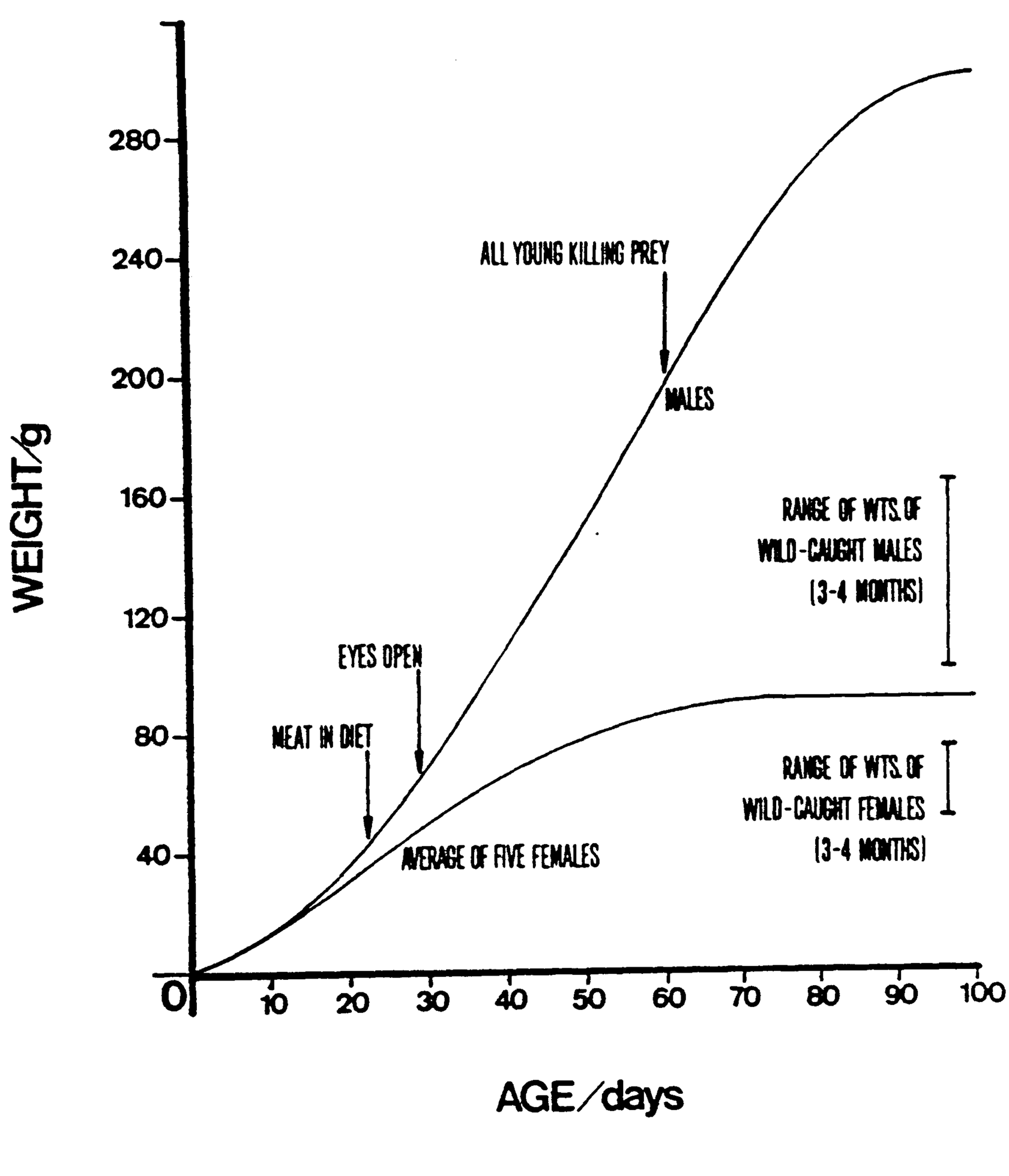
Taylor's (1985) appraisal of the evidence from disease in mankind led him to propose, as a mechanism of sex differentiation, that the Y chromosome codes no specific structural information but normally is the sole mediator of differences in the rate of development of the two sexes. As it permits the expression of genomic information in males to occur more slowly over development it is possible for more genomic information to be transcribed in males than in females. In practice, this means that "a difference in the pace of development between the sexes would become a continuing modulator of further sex differences". The implications for increased male mortality inherent in this 'pace' concept were also remarked: "If the male genome was explored to a greater range of variation, if the slower rate of development allowed greater hazard and advantage, then the human gene pool would be carried at split risk between the more conserving female and the more exploratory male genome. This means that the greater risk would be carried by the more expendable male whose 5% numerical advantage at birth sees him through his period of reproductive life" (Taylor,

1985). Although these conclusions were drawn primarily from examples of disease and mortality in man, there is no reason to doubt their applicabity to sexually reproducing species in general; available data invariably reveal an excess of male over female mortality.

The possibility that large body size may be of differential benefit to males and females is highlighted by the growth tendencies of a group of captive weasels raised on an abundant diet (East and Lockie, 1964). One male and five female weasels shared a common growth rate for about fourteen days only. Subsequently, although still in infancy (preceding the inclusion of meat in the diet and prior to the eyes opening), there was a marked acceleration in the growth rate of the single male which was then maintained for some thirty to forty days after female growth had ceased. Although it would be dangerous to exaggerate the significance of a result based on a comparison of the growth trajectory of a single male and the mean trajectory for five females, it is still tempting to speculate that with an assured and plentiful food supply, sufficient to support a rapid increase in overall body weight, the growth rate of male weasels might well outstrip that of females even at a very early stage in ontogeny. In this particular instance, the divergence in male and female growth rates occurred whilst the infants were still suckling; by this time the mother's food intake had increased to 60g of mouse per day and her weight to

86g whereas prior to pregnancy she had consumed 20-30g of mouse daily at a body weight of 76g. Although the complete developmental picture is not available for wild-caught individuals, the contrasting patterns of intersexual and intrasexual adult body weights between wild-caught and captive animals of some species may be an indication of the profoundly different optimum body sizes which might be favoured by the two sexes in the absence of nutritional constraints (see Figure 4.5). The adult body size of the single captive bred male lies well above the range of values recorded for wild caught males. At the same time, this difference is not only much greater than the intersexual difference between wild-caught males and females but also far exceeds the divergence between the average adult body weight of the five captive females compared with that of wild-caught females within the same age range and also presumably fully grown. It would seem that, even in the absence of nutritional constraints, female weasels exhibit only a modest overall increase in adult body size whereas males have the potential to almost double the characteristic weight they attain in the wild. This finding seems to be somewhat at variance with the early development of lowland gorillas recorded at Jersey Zoological Park (see page 124). Despite the high degree of sexual body size dimorphism between adults, there was no divergence between male and female growth curves during the period from birth to one year, the time span covered by the data. However, the apparent contradiction may be

FIGURE 4.5



Growth and development of weasels

(AFTER EAST AND LOCKIE, 1964)

artificial, since it is not known whether the gorilla infants were given food ad lib. or were constrained by the hand-rearing schedule.

It may be that for certain taxa phylogeny governs both age specific growth rates and ultimate adult body size, allowing only limited variation in either the chronology or magnitude of intersexual differences. There is some evidence of enhanced body size in man, predominantly among males, following an improvement in nutrition and living standards. Differences in stature between parents and same-sexed offspring have been reported for families making socio-economic advance. These were greatest for boys, especially for particularly successful families (Taylor, 1985). This could be the result of higher eco-sensitivity of the developmental process in males, or simply that only a limited increase in size is beneficial to females. It may be that both of these explanations contribute to the recorded facts. Females are certainly better able to withstand a shortage of food than males, a characteristic shared by taxa as diverse as rats, pigs and man (Widdowson, 1976). This capacity is expressed both in differential survival rates and in the varied responses to rehabilitation following starvation and undernourishment. For example, 87% of female pigs survived one year of minimal feeding in contrast to 22% of males; after the same period on a protein deficient diet 83% of females were still alive

compared with 44% of males.

The long term effects of malnutrition also differ between males and females. Widdowson et al. (1964) offered unlimited food to rats which had previously been under-nourished for a period of eight weeks. Although both sexes responded by gaining weight rapidly, the males did not nearly achieve the weight of control littermates, whereas females almost reached this level. There have been comparable findings for humans (Widdowson, 1976; Taylor, 1985). Both sexes suffer retardation in skeletal growth following a period of malnutrition, but females are much more able to redress the deficiency and to catch up at adolescence; as a consequence, sexual dimorphism is reduced in human societies which have experienced a degree of famine. At the same time, the risks and attendant mortality suffered by many young males during premature rapid growth are powerful indicators of the premium attached to large adult body size in males of some species. It may be that the benefits of large adult body size combined with increased eco-sensitivity in males conspires to make them the more vulnerable sex, a tendency which is further reinforced by their typically more aggressive style of interaction. Males are more frequently involved in fights than females, either when seeking entry to a new group or in competing for access to an oestrous female. These contests may be fatal, but in any event, they will be costly in terms of the energy needed for

tissue repair as well as the stress of the actual conflict (Dunbar, 1988).

In general, the dangers of growing too fast, too soon could well be matched by those of growing too little, too late. Although large body size may not be a prime requisite for the female of the species, there is evidence that infant survival is correlated with birth weight (man: Frisch, 1972; deer: Guinness et al., 1978) which might well discourage a smaller female birth weight than the maximimum compatible with maternal well-being. Somewhat surprisingly, a correlation between birth weight and survival was found for males, but not for females, in a captive population of rhesus macaques (Small and Smith, 1986). Even then, once she begins feeding independently, the immature female may be at a disadvantage in inter-specific competition as well as with males of her own cohort if she fails to realise her maximum growth potential.

Since the excess risk carried by young males generally seems to act as a brake on too rapid early growth, the developmental pattern commonly observed in mammals is of an initial phase of roughly equal growth in both sexes, succeeded by more rapid growth of the larger sex in dimorphic species. It may be inferred that the divergence typically occurs at the time of puberty since it is characteristically absent during infancy and the

early juvenile period and is already quite pronounced at first breeding. Once male and female growth curves have diverged, adult size dimorphism generally seems to result from a combination of increased growth rate and extended duration of growth in the larger-bodied sex. For instance, males of sexually dimorphic primate species apparently mature later than the smaller females (see Gautier-Hion and Gautier, 1985). Although data for primates are more freely available, this observation seems to apply to mammals in general (see Figure 3.5) and is consistent with data for cetaceans (Bryden, 1972), which indicate that when the female is the larger sex she attains maturity later than the male.

The ontogeny of sexual size dimorphism has so far been presented mainly in the light of observable facts. To appreciate its significance, these data need to be set in the context of the diverse energetic requirements and life history strategies of male and female mammals in general and primates in particular, with a major role assigned to maternal investment.

4.4 ENERGETIC NEEDS AND MATERNAL INVESTMENT

The growth strategies of both male and female progeny are conditional on the availability and commitment of maternal resources from conception until at least the time of weaning, if not beyond. Indeed, there is evidence that the human infants dimensions at birth reflect almost

entirely the action of the uterine environment and are thus dependent on maternal genotype and maternal-environmental factors only (Tanner, 1960). Consequently, since there are species for which males are already somewhat heavier than females at birth, it is tempting to infer a differential in the degree of prenatal investment on the part of the mother between sons and daughters.

Yet females are typically born at a more advanced stage of maturation, e.g., in terms of skeletal development, a sex difference which persists through to adulthood and occurs in chimpanzees, rhesus monkeys, rats and perhaps all mammals (Tanner, 1960) as well as in birds (Richter, 1983). This raises the possibility of intersexual differences in the partitioning of the available energy between the various processes of growth and maturation as well as, or perhaps instead of, differences in the overall energy expended. Even within a single individual, different aspects of maturation may proceed independently. For instance, Demirjian (1978) found no correlation between dental and skeletal maturity, so that to focus exclusively on a single aspect of growth and maturation, viz. size, may result in the neglect of a mosaic of other less obvious ontogenetic processs, all of which presumably require an energetic input. It is quite conceivable that, even prenatally, it is the developing individual that manipulates the total resources at its disposal, selectively investing these according to

priorities determined by the interaction of phylogeny, species and sex.

This possibility accords with the rather limited data available on birth weight, gestation period and subsequent interbirth interval. Whilst an increase in the interbirth interval, seemingly determined by the sex of the preceding infant, may suggest an increased investment in that sex, either prenatally or in the immediate postnatal phase, the weight of the last born infant does not appear to be the sole determinant of interbirth interval. Among red deer and some other ungulates, mothers of male calves are more frequently barren the subsequent year than mothers who have given birth to females, which are lighter and presumably less costly to rear (Clutton-Brock and Albon, 1982); elephant births appear to follow a similar pattern in that females with a surviving son tend to have longer interbirth intervals than females with a surviving daughter (Lee & Moss, 1986). In contrast, a study of captive macaques indicated that: "mothers of male rhesus infants, which are the slightly heavier sex at birth, ... conceive again sooner" (than mothers of females), a rather surprising result which is corroborated by data from other captive colonies but not replicated in either of two free-ranging populations studied over a long period (Simpson et al., 1981).

These findings are somewhat at variance with

Richter's (1983) observation that "males may receive considerably more food than females only when parents are not limited in how much food they can deliver in a day. In the absence of such a limitation male and female offspring will result in the same cost to future reproduction, regardless of their differences in energy requirements". On this basis there should, of course, be no difference in interbirth interval following the birth of a male or female macaque in captivity, presuming the absence of nutritional constraint. It has also been observed that male elephant calves attempt to suckle more often, are more successful in their attempts and are as well tolerated by their mothers as are the less demanding female calves. It follows that male calves are likely to have a higher nursing intake than female calves during the wet season, when readily available resources enable mothers to produce milk freely. It has further been remarked that under these favourable conditions there is little intersexual difference in survivorship, whereas during drought years, when the mother's food consumption is inadequate to sustain her milk yield at the level needed by her son, mortality rates of young males exceed those of females (Lee & Moss, 1986). It follows that, in the absence of resource limitation, if the mother's nutritional plane were the sole consideration, then there should be no difference in the interbirth interval following the birth of a male or female infant. Yet differences in interbirth interval persist, among species

as varied as elephants and macaques. Although these differences appear to be mediated by the sex of the last born infant, the evidence from macaques suggests that they may not always be attributable to intersexual differences in neonatal body weight.

In seeking an explanation, it is probably an over-simplification to regard intersexual variation in interbirth intervals solely as a response to differences in the energetic needs of males and females. This approach makes no allowance for the complexities of maternal-infant interactions among mammals. Simpson and his associates suggest that macaque mothers both respond to and test the progress of their infants, conceiving earlier the better this progress seems to be, so that the greater activity of sons at two weeks would tend to promote an earlier subsequent conception. Moreover, both rhesus and pigtail macaque mothers carrying male fetuses are less subject to threats, chases and attacks than those carrying females (Simpson et al., 1981). Since this would tend to reduce the mother's prenatal energy expenditure it might also be a contributory factor.

In addition, environmental conditions will influence the scale of the maternal investment that can safely be devoted to the developing embryo. It is clearly maladaptive for a mother to commit so much energy to the prenatal growth and development of her infant that she is

unable to sustain its postnatal demands, or can only do so to the detriment of her own future reproductive success. Moreover, once weaned, the immature individual must be able to obtain sufficient food to support the body size it has attained. Despite relative economies of size, larger animals require absolutely more food. The excess mortality observed among fast growing young males compared with same-aged females of the same species highlights the increased risks associated with this strategy (see pages 128-130). It will probably be most successful in a relatively r-selecting environment which grants surviving individuals the opportunity to achieve an enhanced adult body size although the less successful animal is liable to fail utterly. Indeed, it is males of such species which show the greatest variability in reproductive performance and it would appear that, in the survival stakes, the greatest potential is associated with the highest risk.

The patas monkey, Erythrocebus patas, affords a convincing example of the interdependence of growth and life history parameters and the environment. Male patas are heavier at birth and immediately grow more rapidly than females (see page 126 and Figure 4.4). There is extreme sexual size dimorphism between adults and these monkeys are among the most r-selected primates in terms of a whole mosaic of associated characters (C. Ross, pers. comm.). The discrepancy between the ages at which males and females attain sexual maturity is also quite

pronounced and the species is characterised by an enhanced degree of maternal investment (see below). The potential of a young mother to achieve a high level of investment must surely be conditional on the quality of the habitat she occupies, a factor which also has far-reaching consequences for intersexual relations and overall social strategy and organisation. It therefore seems likely that a reduction in the age at first breeding and an increase in maternal investment will both arise in conjunction with sexual size dimorphism, to an extent which mirrors the degree of overall dimorphism attained. Patas monkeys merely represent an extreme in the development of this tendency, with females reaching sexual maturity at an earlier age than is typical of any other cercopithecine for which there is adequate field and laboratory data (Rowell, 1977).

Martin and MacLarnon (1985) have already shown that, during gestation, mothers of altricial mammals typically invest more per day in their offspring than mothers of precocial infants. Since it is hypothesised that sexual dimorphism arises in response to relative r-selection, the same differential should arise between maternal investment in dimorphic and monomorphic primate species. The present approach follows Martin and Maclarnon in using the fetal growth factor as the best reflection of "the differential capacity for investment in fetal growth exhibited by mammalian mothers of different body sizes when other

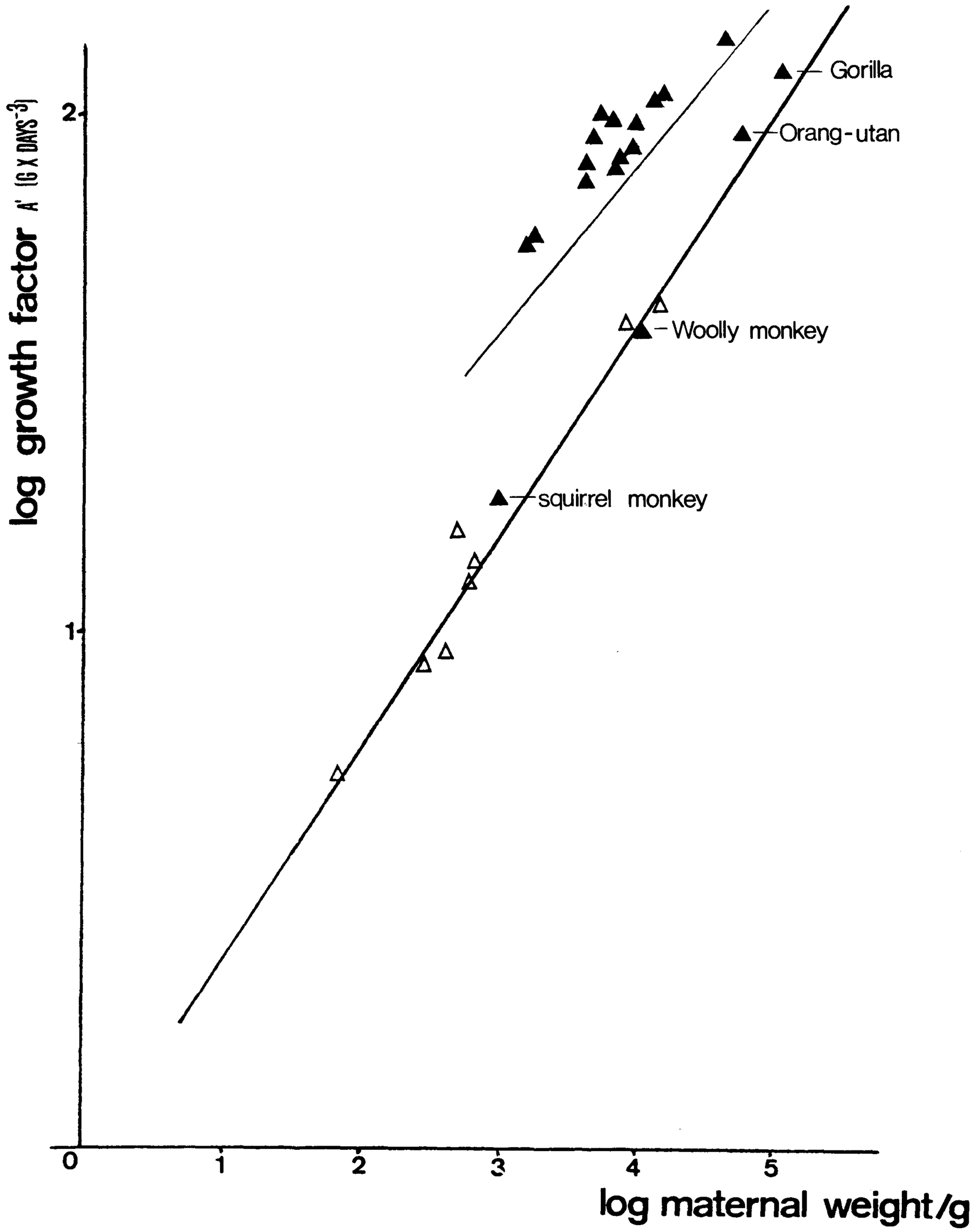
things are equal".

The 'fetal growth factor' is a valuable comparative measure that can be used freely, irrespective of differences in overall body size. Otherwise, interspecific comparisons of prenatal maternal investment are particularly vulnerable to the confounding effects of scaling to body size since both gestation period and neonatal body weight are allometrically related to maternal body weight (see summary tables in Calder, 1984 and Peters, 1983). However, Martin and MacLarnon (1985) showed that the overall scaling of neonatal weight to maternal weight can be expressed in a combined formula that takes account of both the duration and rate of allocation of maternal resources, thus enabling levels of maternal investment to be compared between females of widely different adult body sizes.

The standard fetal growth formula, $W_F = a.(t-t_o)^3$, relating fetal weight (W_F) to time elapsed (t), following an intitial time 'lag' (t_o), was theoretically derived by Payne and Wheeler in 1967 and corroborated by their own empirical observations as well as those of several other studies (e.g., Huggett and Widdas, 1951; Roberts and Perry, 1974). For a neonatal body weight of W_N, following a gestation period G, the formula becomes $W_N = a.(G-t_o)^3$, which reduces to $W_N = a'.G^3$, since t_o is small in comparison with G. Previous studies have shown that both a

and a' exhibit systematic allometric variation with maternal body weight (Rudder, 1978, 1979; Martin and MacLarnon, 1985). Moreover, Martin and MacLarnon (1985) have also successfully exploited the scaling of a' to differentiate between the relative levels of maternal investment which typically characterise altricial and precocial mammals. In a similar vein, and again calculating a' as W_N/G^3, the data of the present study were analysed to determine whether a comparable dichotomy existed between dimorphic and monomorphic species in terms of their proportional allocation of maternal resources to fetal growth. It was predicted (page 145) that this would be greater for females of dimorphic species than for those of monomorphic species.

To test the concurrence between expectation and observation, a logarithmic plot of fetal growth factor values (a') against maternal weights was examined for a sample of 28 simian primates (see Figure 4.6). The major axis derived gave a scaling exponent of 0.55 relating maternal weight and fetal growth for the complete sample. However, there was a clear separation between the distributions of dimorphic and monomorphic species about the combined major axis, and when separate major axes were calculated for each of the two groups somewhat lower gradients were obtained, namely, 0.43 and 0.33 for monomorphic and dimorphic species respectively (See Table 4.2). The striking difference in the intercepts, -0.05 for



Log fetal growth factor VS. **log maternal body weight for simian primates.**

TABLE 4.2

PRENATAL MATERNAL INVESTMENT

LOG NEONATAL WEIGHT vs LOG MATERNAL WEIGHT

	n	b	a	95% C.I.	R
ALL SIMIAN PRIMATES	28	0.78	-0.34	0.73 - 0.84	0.99
MONOMORPHIC SPECIES	9	0.78	-0.39	0.69 - 0.89	0.99
DIMORPHIC SPECIES	19	0.67	0.15	0.55 - 0.74	0.98

LOG FETAL GROWTH FACTOR vs LOG MATERNAL WEIGHT

	n	b	a	95% C.I.	R
ALL SIMIAN PRIMATES	28	0.55	-0.27	0.43 - 0.68	0.87
MONOMORPHIC SPECIES	9	0.43	-0.05	0.30 - 0.55	0.94
DIMORPHIC SPECIES	19	0.33	0.64	0.17 - 0.51	0.71

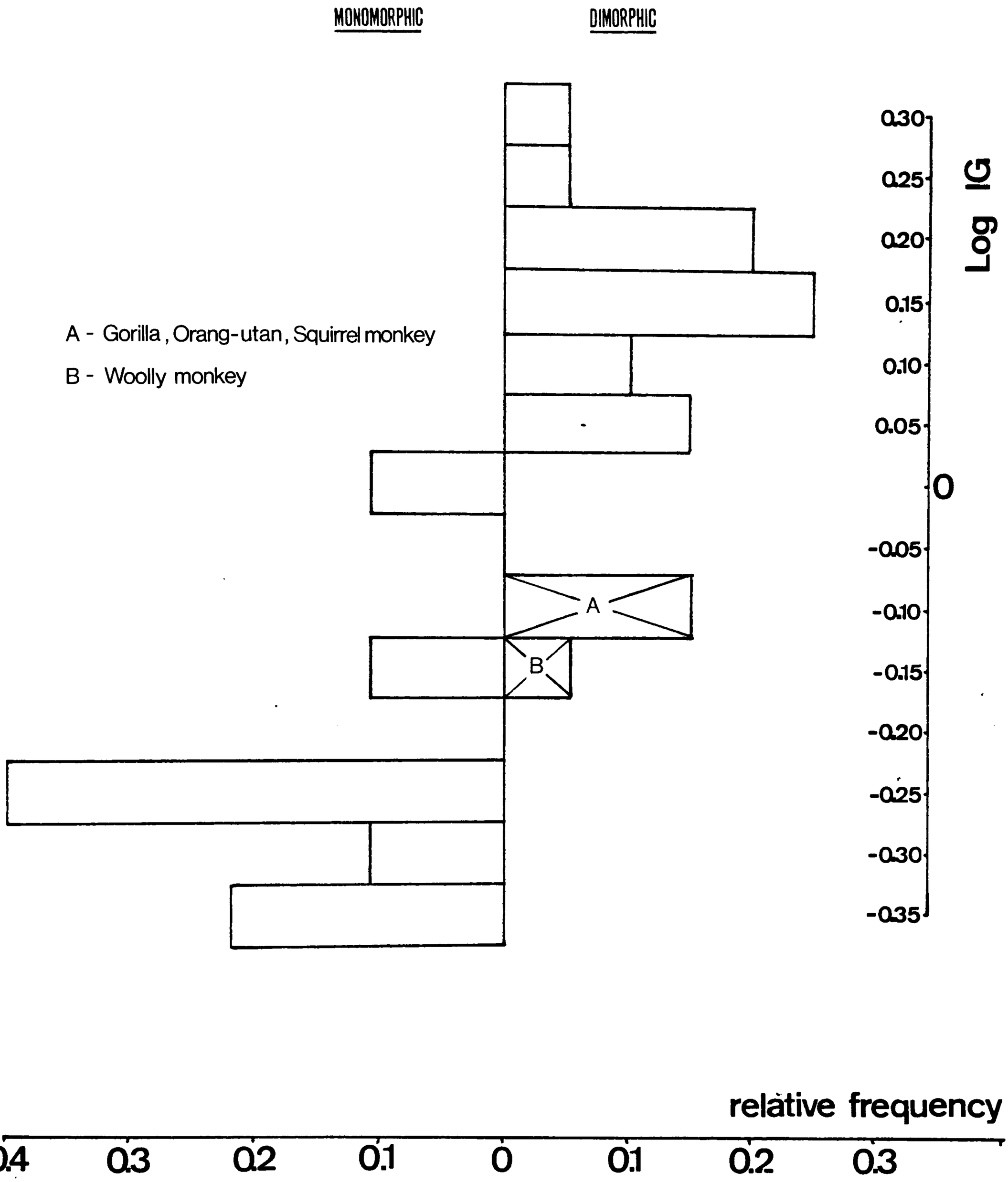
LOG AVERAGE FETAL GROWTH vs LOG MATERNAL WEIGHT

	n	b	a	95% C.I.	R
ALL SIMIAN PRIMATES	28	0.70	3.70	0.63 - 0.77	0.97
MONOMORPHIC SPECIES	9	0.66	3.73	0.55 - 0.79	0.99
DIMORPHIC SPECIES	19	0.55	4.33	0.43 - 0.63	0.96

b = gradient (i.e. allometric exponent)
a = intercept of major axis
R = correlation coefficient

monomorphic species and 0.64 for dimorphic species reinforced the visual impression of a grade distinction, implying a divergence in the daily levels of maternal investment between these two categories of primate. In addition, for each of the two groups taken separately, one gradient coincided with the lower boundary of the 95% confidence interval for the combined data set, the other fell below this limit. The subsequent analyses were therefore based on a common axis passing through the mean of the complete sample and with a gradient of 0.38, this being the mean of the slopes obtained for dimorphic and monomorphic species (0.33 and 0.43 respectively). Using the logarithmic index of fetal growth, Log IG, defined as the displacement of the actual species point from the chosen axis (see page 52), a significant difference was found between the mean indices of monomorphic and dimorphic species (t-test; $p<0.0005$).

However, despite the highly significant difference between the mean indices of maternal investment for monomorphic and dimorphic species, a comparison of summary statistics can obscure aspects of the data that warrant closer examination (see Figure 4.7). It would appear that gorilla, orang-utan, squirrel and woolly monkey mothers each tend to invest less in their infants than do other dimorphic females, at least in terms of measurable prenatal input. However, both squirrel and woolly monkeys are only mildly dimorphic. In contrast, although neither



Maternal investment in 9 monomorphic and 19 dimorphic species. Bar charts of relative frequencies of log IG values.

gorilla nor orang-utan indices are significantly aberrant, they yield somewhat higher values than might have been expected for such extremely size dimorphic species. It may be that the reduced maternal investment of these large primates is linked to their rather poor diets, which cannot sustain the heightened metabolic rate which other females attain during pregnany. The mountain gorillas of the Eastern region are almost certainly folivorous, since they live at altitudes beyond the range of fruiting trees (R.I.M. Dunbar, pers. comm.). West African gorillas may eat some fruit, but they are still primarily frugivores, while orang-utans mainly eat unripe fruit (e.g., figs). R.D. Martin (Pers. comm.) suspects that both species have low metabolic rates, in keeping with the poverty of these animals' primary food sources and certain characteristics found in their haemoglobin which are usually associated with a slow metabolism.

Absolute body size might also influence the allocation of maternal resources in such particularly large primates. Martin and MacLarnon (1985) have remarked a 'ceiling' effect for maternal investment. The allometric exponent itself appears to vary with body weight, tending asymptotically to a limit. This suggests that, for large species, there may be an upper threshold beyond which further investment of maternal resources would cease to be adaptively advantageous.

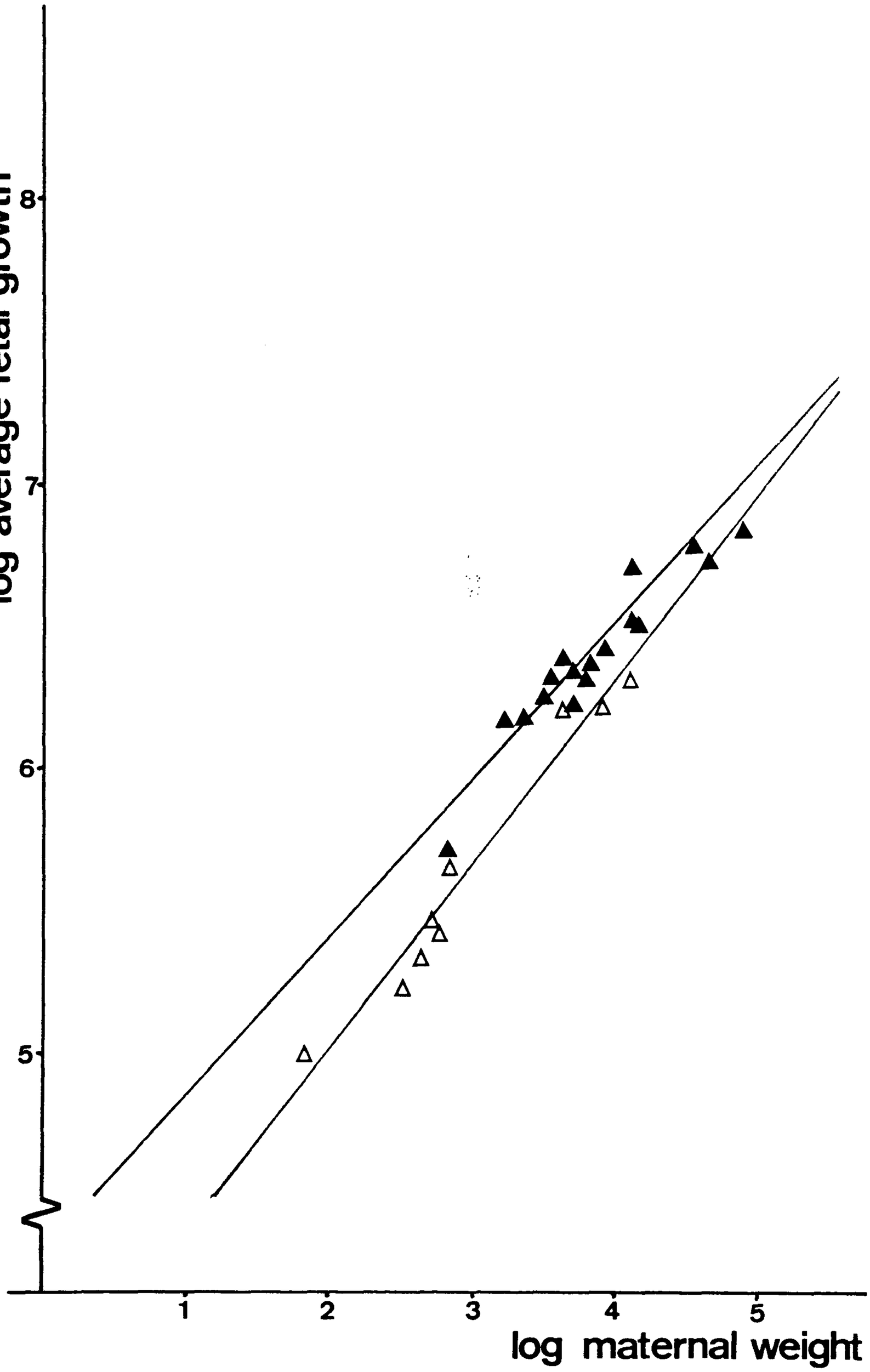
Nevertheless, even with the inclusion of data for possibly 'exceptional' species, the major axes calculated separately for dimorphic and monomorphic species (see Figure 4.6 and Table 4.2), each showed a clear vertical displacement relative to the previously obtained common axis, with a shift upwards for dimorphic species and downwards for monomorphic species. This was despite the influence of data for gorilla and orang-utan which, on account of their large body size, clearly depressed the major axis slope for dimorphic species. It seems that neonates of sexually dimorphic species have enjoyed a higher level of prenatal investment than those of monomorphic species.

In a subsequent conference paper (unpublished), Martin and MacLarnon departed from the use of the fetal growth factor a' on the grounds that it reflects a basic 'setting' for an individual species without giving a clear indication of the average cost to the mother throughout gestation. They now advocated reverting to the approach originally suggested by Payne and Wheeler (1967) and preferred the use of neonatal weight divided by gestation period as the measure of maternal investment (R). It was considered unlikely that revising the measure of maternal investment would materially affect the present conclusions, since these derived from a comparison of monomorphic and dimorphic species, referred to a common basis. Nevertheless, the analyses were repeated, using

$R=W_N/G$ instead of a' and the previous findings were corroborated. A marked grade effect was apparent between monomorphic and dimorphic species, with the major axis calculated for the entire sample of simian primates having a higher gradient than the axes calculated independently for monomorphic and dimorphic species (see Table 4.2 and Figure 4.8). The separate gradients for the two groups were 0.62 and 0.66 respectively, and since these did not differ significantly, the average of 0.64 was adopted as the gradient for an axis passing through the mean of the complete sample. This axis was then used to obtain indices for the average commitment of maternal resources, Log IR, just as the major axis for a' had previously been used to calculate Log IG values. The results showed the same clear dichotomy beween monomorphic and dimorphic species which had emerged from the original calculations. The mean index for dimorphic species was again significantly greater than the mean for monomorphic species ($p < 0.001$). Gorilla and orang-utan once more appeared somewhat aberrant, with lower than expected investments. The use of an alternative measure called for no revision of the earlier conclusions. Maternal investment seemed typically to be significantly greater among dimorphic species than monomorphic species, whichever criterion was chosen to measure it.

There is unfortunately a paucity of data covering maternal investment during the postnatal developmental period prior to weaning, although it is well known that

FIGURE 4.8



Log average fetal growth vs. log maternal body weight.

females expend more energy when lactating than at any other time. For instance, Coelho (1974) inferred, from indirect evidence obtained with captive animals, that the energetic needs of a female Sykes monkey, Cercopithecus albogularis, increase by an estimated 25% during pregnancy and 50% when lactating. In addition, from their examination of the stomach contents of a number of animals, Laws et al. (1975) concluded that elephants with suckling calves eat twice the amount consumed by any other class of elephant, notwithstanding the much greater size of the adult males and the presumably enhanced needs of immature males during their most rapid growth phase. Kenagy (1987) also found that, among golden mantled ground squirrels, the daily energy expenditure of females during lactation was greater than that of any other age or sex class at any time of year. However, there is insufficient information to permit comparison between the nutritional needs of dimorphic and monomorphic mothers during the early months or years of their infants' lives. It would be of interest to monitor the food intake of adult females from a range of species both before and in the course of pregnancy as well as whilst lactating. All the same, it seems logical to assume that dimorphic females, which have already achieved a greater degree of prenatal maternal investment, should also maintain a higher level of postnatal investment than females of monomorphic species(see p. 262). The partitioning of this enhanced resource between the processes of growth and maturation might then depend on

the sex of the infant (see pages 140-141).

Once weaned, the still immature individual will then experience the full thrust of competition with other group members as well as possibly with animals of other species. Now there may well be a continuing element of parental investment at this stage on the part of the mother or father or both, but this is likely to be quite difficult to detect and virtually impossible to quantify since it will most probably find subtle forms of expression. The benefits derived from shared territories and toleration or protection at feeding sites do not readily lend themselves to measurement; and whilst the acceptance of juveniles within a parental territory is mainly the prerogative of monogamous species, immature members of dimorphic species may gain protected access to limited resources by being permitted to feed in proximity to one or both parents. Each of these scenarios represents a form of continued investment on the part of the adult(s) involved as they arguably reduce the resource available to the older animal(s). Then, since the style of parental support will almost certainly depend on the social structure of the species concerned and this, in its turn, will tend to differ between dimorphic and monomorphic species, the whole issue becomes hopelessly confounded and viable comparison of maternal/parental investment across the two groups is effectively precluded.

In several species (viz. chimpanzees) kinship bonds and mutual, reciprocal investment continue to be an important factor throughout maturation and into adulthood. Although such considerations mainly lie outside the scope of the present study, several features which promote sexual dimorphism in adult body size are inseparable from the wider aspects of life history strategy. Some of these were discussed in Chapter 3, when it was argued that intersexual differences in adult body weight had been promoted by earlier sexual maturation of females at a smaller adult body size. The next chapter describes how brain size allometry can be used to defend this hypothesis and establish that females of sexually size dimorphic species have experienced a reduction in mature adult body weight, sometimes, but not always, accompanied by an increase in male body size. This original analysis is preceded by a brief outline of the intersexual differences that have emerged from studies of the organisation of the brain.

CHAPTER 5

SEXUAL DIMORPHISM AND THE BRAIN

5.1 OVERVIEW

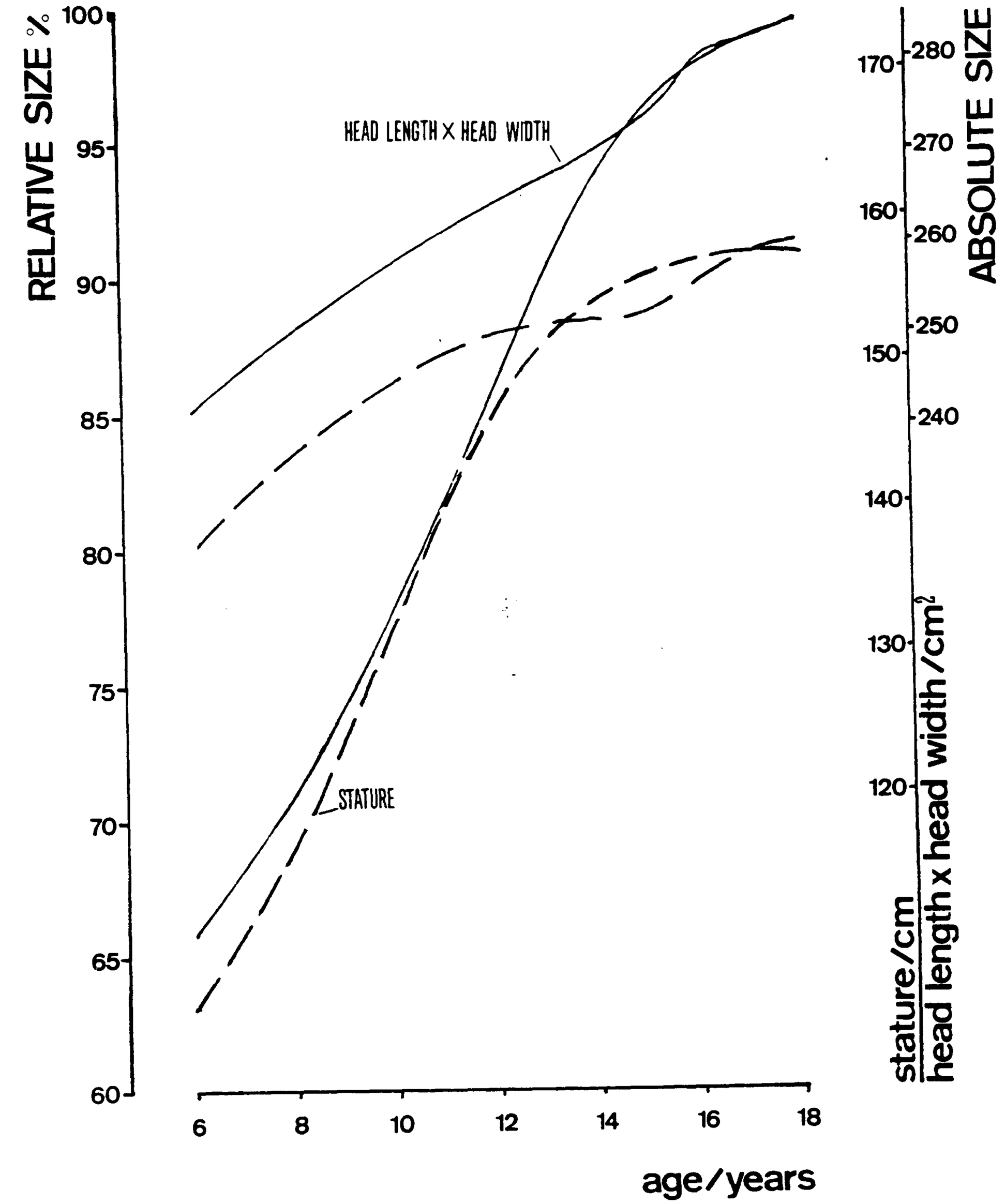
There is an element of sexual dimorphism in both the weight and internal organisation of the brain. Pakkenberg and Voigt (1954) gave mean brain weights of 1440g for men and 1282g for women based on a sample of 765 male and 325 female cadavers. This yields a male:female brain weight ratio of 1.12 as compared with an overall body size dimorphism of 1.18 in humans.

Baughan and Demirjian (1978), accepting the dictum that "it is growth of the brain that determines cranial shape and expansion, rather than vice-versa", used the product of cranial length and width as an external measure to replace brain weight in a longitudinal study of two cohorts of school-age children. In fact, the suitability of this measure is shown by actual data on brain weight and cranial capacity (R.D. Martin, pers. comm.). Although Baughan and Demirjian did not propose a conversion factor to transform their measure into either a true volume figure for cranial capacity or an estimate of brain weight, this does not detract from its usefulness in a comparative study. Moreover, it has the merit that observations need no longer be confined to a morbid population, as in the case of brain weight, and that

sequential data can be collected from an appropriately large sample of healthy individuals. Measurements drawn from 109 boys and 101 girls indicate that there is already a significant degree of sexual dimorphism in cranial dimensions even among six year olds, the youngest age of children included in the study. From the graph (Figure 5.1), based on Baughan and Demirjian (1978), it is clear that sexual dimorphism in brain size precedes the incidence of sexual dimorphism in body size. In addition, the magnitude of the difference between male and female brain size attained at this early stage in development is maintained at the same level throughout the pubertal growth period, irrespective of sexual differences in overall growth rate. Brain growth appears to follow the same linear trend for both sexes and to be independent of non-linear changes in stature of either boys or girls. It seems that by the age of six years at latest, and perhaps even sooner, male and female brain weights are targeted at different adult values. This may be related to the rapid growth of the brain both prenatally and during the early postnatal period and to its subsequent much slower development, a feature shared to some extent by man and non-human primates (see Figure 5.2).

However, as Kerr et al. (1974) have cautioned, "many factors which influence fetal and postnatal growth (uterine and placental structures, maternal:fetal weight ratios, growth velocities, etc.) show important

FIGURE 5.1



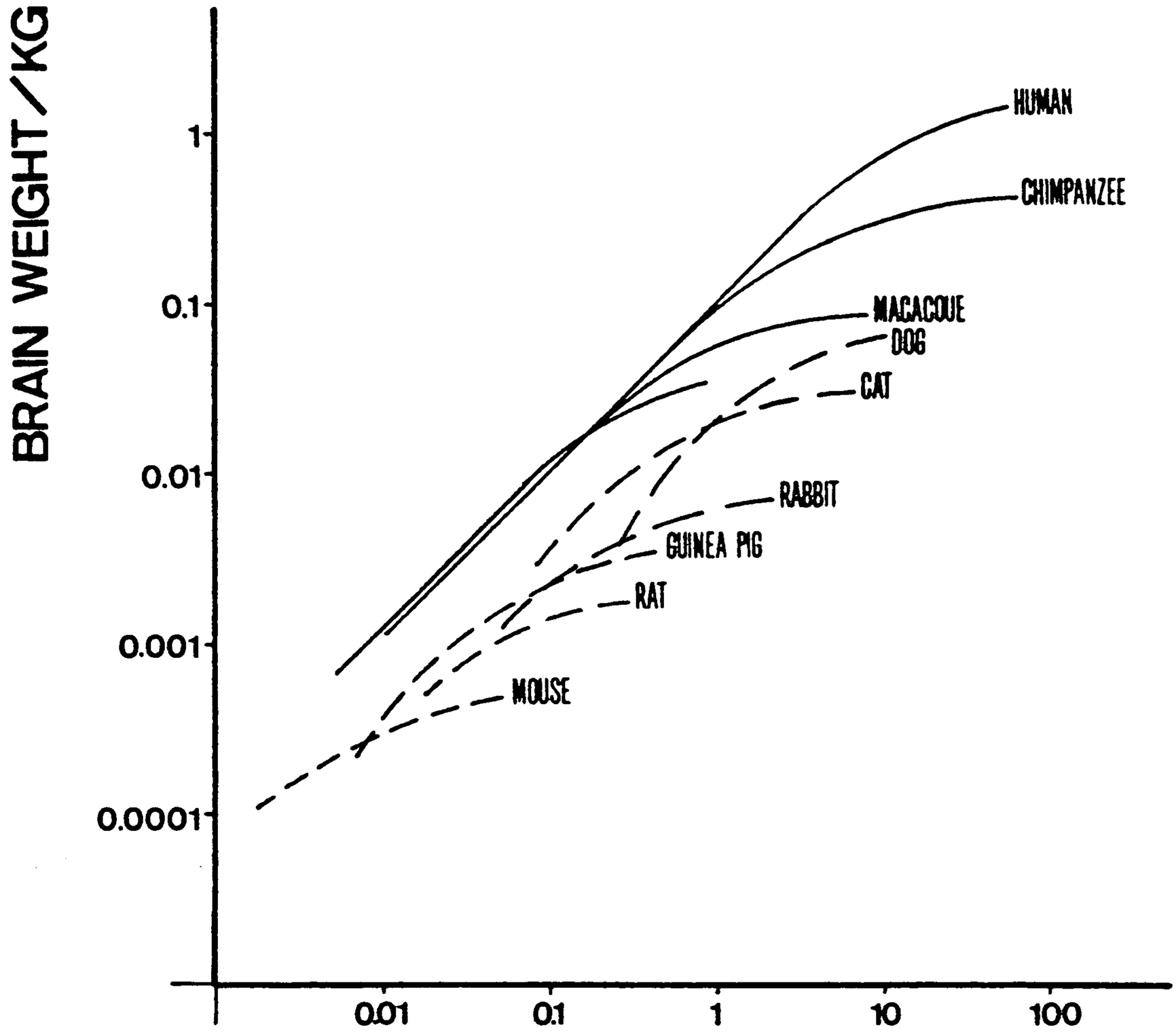
GIRLS — —

BOYS ——

Mean growth curves for the product head length x width and for stature of Montreal boys and girls

(AFTER BAUGHAN & DEMIRJIAN, 1978)

FIGURE 5.2



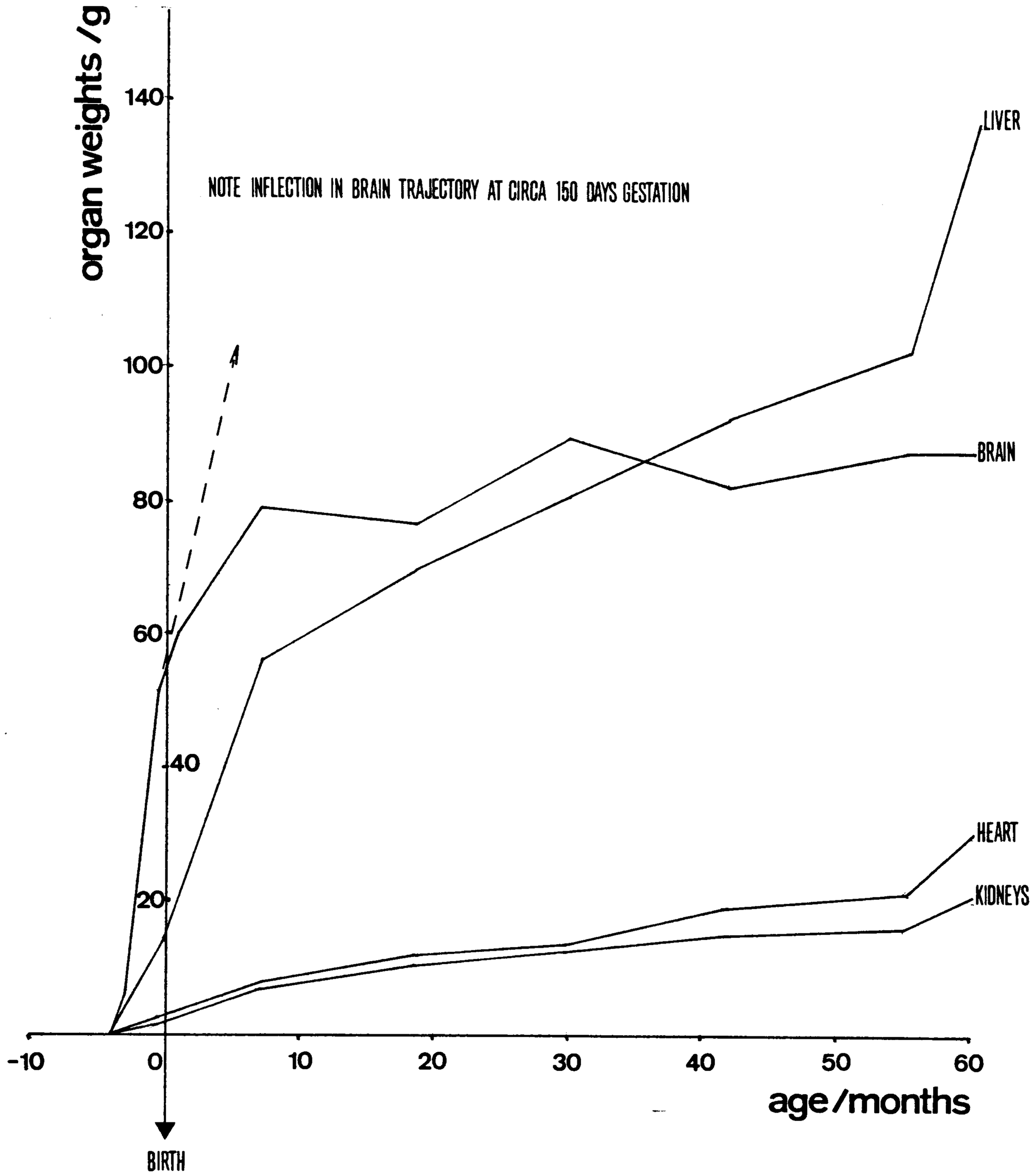
(NOTE GRADIENT OF PRIMATE TRAJECTORY)

Logarithmic plot of brain weight against body weight for primates and non-primate mammals from fetal life through development to adulthood. (AFTER HOLT ET AL., 1975)

differences between primates and sub-primate species, and there are grounds for concern that data collected from the latter species may not be applicable to man". Although man is much closer to nonhuman primates than to nonprimate mammals, the dangers of extrapolation remain, even when using monkeys or apes as models. For instance, the special pattern of human brain growth in the first twelve months of postnatal life is a feature unique to man (see Figures 5.2 & 5.3). Nevertheless, many shared aspects of fetal environment and early growth enable primate studies to yield valuable insights into processes of biological growth in man. Yet the analogy should not be pressed too far; a mosaic of shared characteristics does not diminish the significance of those attributes which differentiate between two taxa. The remarkably large size of the adult brain relative to body size is probably the single most distinguishing human feature, so it is scarcely surprising that differences in growth pattern arise between man and primates. Such differences are not only predictable, but also call for further study.

Nevertheless, the apparent absence of sexual dimorphism in brain weights and birth weights typically reported for non-human primates, in contrast to man, probably stems from the paucity of the available data rather than from a genuine absence of the phenomenon. Species' means are commonly based on data of uneven quality, drawn from various sources and gathered by

FIGURE 5.3



Organ growth in rhesus monkeys (DATA FROM KERR ET AL.1974)

different investigators (see 2.4.1). These factors generate high levels of within group variability which are liable to mask moderate intergroup differences unless offset by large sample sizes; indeed, a statistically significant sexual dimorphism in human birth weights was established only on the evidence of 23,970 live births (Gibson and Mackeown, 1952). Since sample sizes tend to be small when measurements require animals to be sacrificed, real differences of small absolute magnitude are likely to remain undetected. Kerr et al. (1974) identified this problem in their study of rhesus monkeys: "The limited number of animals and the wide range of values for organ weights at each age masked any sex-associated pattern of organ growth: data from male and female animals were therefore combined." The same difficulty has been encountered during the present study and is discussed below, in relation to allometric analysis of the brain to body weight relation (5.4).

It would clearly be of great benefit to have data from larger samples. Perhaps, following the practice adopted by Baughan and Demirjian (1978), it will also prove feasible to infer cranial capacity or brain weight from the external skull dimensions of nonhuman primates. In addition, modern X-ray techniques may eventually permit brain scans to be performed on large numbers of colony reared animals of known ages. Research of this nature should afford further insight into both the inception and

extent of sexual dimorphism in the nonhuman primate brain and could possibly be undertaken on captive bred marmosets and rhesus monkeys, which are already maintained in well established colonies.

5.2 BRAIN SIZE AND BODY SIZE: THE GENETIC LINK

The link between brain size and adult body size seems subject to considerable flexibility. This becomes apparent when the interrelation between these variables is examined for a sample of males and females from closely related species (see Table 5.1). Logarithms of brain weights were plotted against the corresponding logarithms of body weights for several cercopithecine species (see Figure 5.4). Data were available for males from 7 species and for females from 6 of the same species. Major axes and correlation coefficients were calculated for the combined data set as well as separately for each sex. The correlation coefficient based on female data alone failed to attain significance even at a 0.10 level, whereas the coefficients calculated for males alone and for males and females taken together were both highly significant ($r = 0.92$, $p < 0.005$ and $r = 0.78$, $p < 0.005$, respectively). There appears to be no association between brain size and adult body size for females of closely related cercopithecine species, an insight which is totally obscured when data from both sexes are combined. Findings of this nature, which differ between males and females, are especially vulnerable to the exigencies of

TABLE 5.1

ALLOMETRIC RELATIONS FOR BRAIN WEIGHT AND BODY WEIGHT FOR MALES AND FEMALES OF CLOSELY RELATED SPECIES

CERCOPITHECINES

	LOG. BODY WT.	LOG. BRAIN WT.	LOG EQ
MALES			
Cercopithecus aethiops	3.688	4.835	-0.012
Cercopithecus ascanius	3.631	4.841	0.016
Cercopithecus l'hoesti	3.929	4.968	0.028
Cercopithecus mitis	3.868	4.900	-0.016
Cercopithecus mona	3.643	4.841	0.011
Cercopithecus nictitans	3.819	4.875	-0.023
Cercopithecus pygerythrus	3.731	4.861	-0.003
FEMALES			
Cercopithecus aethiops	3.540	4.779	-0.033
Cercopithecus ascanius	3.469	4.787	0.000
Cercopithecus l'hoesti	3.672	4.927	0.070
Cercopithecus mitis	3.631	4.752	-0.091
Cercopithecus mona	3.398	4.792	0.029
Cercopithecus pygerythrus	3.480	4.818	0.026

CATEGORY	(n)	GRADIENT	INTERCEPT	CORRELATION COEFFICIENT	SIGNIFICANCE
MALES	(7)	0.387	3.421	0.920	P < 0.005
FEMALES	(6)	0.343	3.600	0.429	n.s.
MALES + FEMALES	(13)	0.323	3.663	0.780	P < 0.005

MACAQUES

	LOG. BODY WT.	LOG. BRAIN WT.	LOG EQ
MALES			
Macaca arctoides	4.002	5.007	-0.043
Macaca fascicularis	3.740	4.852	-0.021
Macaca mulatta	3.804	4.954	0.038
Macaca nemestrina	3.998	5.073	0.026
FEMALES			
Macaca arctoides	3.931	4.999	-0.064
Macaca fascicularis	3.558	4.793	-0.027
Macaca mulatta	3.736	4.928	-0.008
Macaca nemestrina	3.745	5.041	0.099

CATEGORY	(n)	GRADIENT	INTERCEPT	CORRELATION COEFFICIENT	SIGNIFICANCE
MALES	(4)	0.674	2.351	0.913	P < 0.05
FEMALES	(4)	0.653	2.497	0.778	n.s.
MALES + FEMALES	(8)	0.558	2.826	0.800	P < 0.01

Continued...

TABLE 5.1 Continued

BABOONS

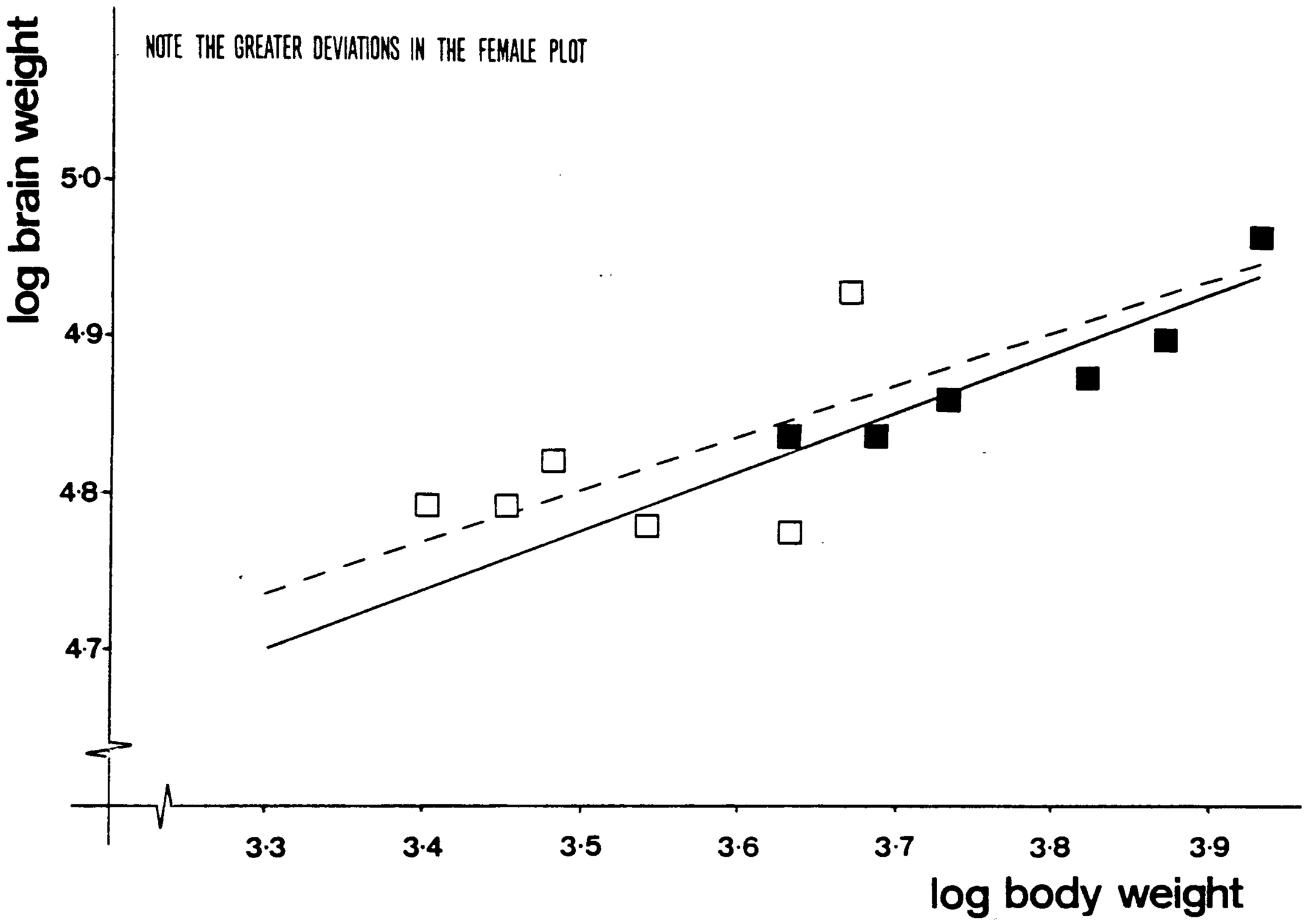
MALES	LOG. BODY WT.	LOG. BRAIN WT.	LOG EQ
Papio cynocephalus	4.337	5.257	0.022
Papio hamadryas	4.254	5.226	0.073
Papio papio	4.279	5.286	0.108
Papio ursinus	4.457	5.258	-0.098
Theropithecus gelada	4.288	5.083	-0.104
FEMALES			
Papio cynocephalus	4.062	5.215	0.060
Papio hamadryas	4.000	5.154	0.053
Papio papio	4.209	5.283	0.001
Papio ursinus	4.169	5.216	-0.032
Theropithecus gelada	4.068	5.078	-0.082

CATEGORY (n)	GRADIENT	INTERCEPT	CORRELATION COEFFICIENT	SIGNIFICANCE
MALES (5)	1.002	0.888	0.272	n.s.
FEMALES (5)	0.866	1.639	0.690	n.s.
MALES + FEMALES (10)	0.312	3.892	0.448	n.s.

LESSER APES

MALES	LOG. BODY WT.	LOG. BRAIN WT.	LOG EQ
Hylobates agilis	3.772	4.968	-0.022
Hylobates lar	3.752	5.017	0.037
Hylobates moloch	3.776	4.977	-0.015
Symphalangus syndactylus	4.045	5.123	-0.000
FEMALES			
Hylobates agilis	3.743	4.943	-0.018
Hylobates lar	3.738	4.973	0.015
Hylobates moloch	3.753	4.969	0.003
Symphalangus syndactylus	4.024	5.114	-0.001

CATEGORY (n)	GRADIENT	INTERCEPT	CORRELATION COEFFICIENT	SIGNIFICANCE
MALES (4)	0.486	3.156	0.930	$P < 0.05$
FEMALES (4)	0.549	2.907	0.984	$P < 0.01$
MALES + FEMALES (8)	0.523	3.009	0.955	$P < 0.01$



males■ and male axis ——
females□ and female axis– – –

Plot of log brain weight against log body weight for male and female cercopithecine species together with principal axes

insufficient data which cannot adequately support separate analyses by sex. This is a pervasive handicap in the study of sexual dimorphism. However, in this instance, analysis of male and female data drawn from four species of macaques corroborated the results obtained for cercopithecines. No significant correlation was found for females alone whilst the correlation coefficients for males alone and for males and females taken together were again significant ($r = 0.80$, $p < 0.01$ and $r = 0.91$, $p < 0.05$, respectively).

One response to this finding could be to question the quality of the female body weight data from which it derives. Although body weight estimates for both sexes were based on comparable sample sizes, those available for females are often prone to greater variability due to reproductive status. Of course the initial raw data were screened, in an attempt to exclude weights recorded for immature, sick, obese or underweight animals, or for pregnant females (see 2.4.1). However, there is no certainty that this aim was achieved. At the same time, a potentially revealing anomaly should not be ignored because it <u>might</u> merely be an artefact of inadequacies in the data. Possible explanations for the lack of association between brain size and adult body size noted uniquely for females, but not for males, in each of two sexually dimorphic genera are considered in conjunction with the results of allometric analyses (see 5.4; pages

218-219). The absence of any significant correlation between brain weight and adult body weight for either males, females or males with females among 5 species of baboon is also examined.

The lack of a significant correlation between brain weight and body weight among animals of related species, although it has here been observed only for cercopithecine and macaque females, has far-reaching implications. Even a single example would be sufficient to indicate a somewhat loose genetic link between brain size and adult body size. Such an apparent uncoupling of brain weight and body weight might have arisen as a consequence of the continued growth in overall body size that follows the developmental stage at which brain growth is virtually complete (Kerr et al., 1974; Falconer, 1981; Lande, 1981; Shea, 1983; Holt et al., 1975; Martin and Harvey, 1985).

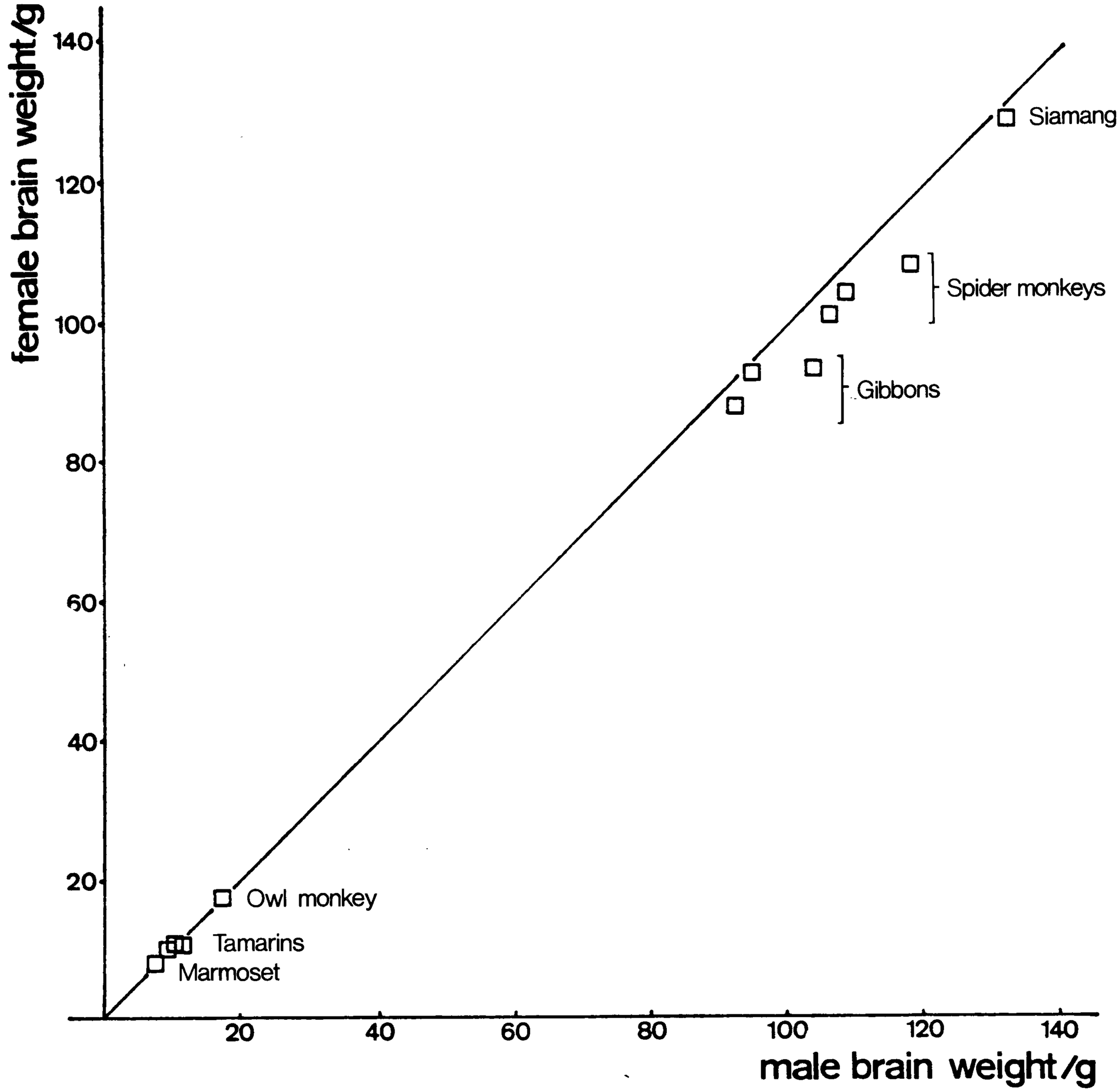
Lande (1985) cited "genes that act late in development to change the relative growth rates of different organs" and "produce small, quantitative variations that are the basis for most morphological evolution in higher animals". By the time such variations could take effect, the brain might well have almost attained its mature target size. Lande further suggests that for "species with extended parental care of offspring, individuals are shielded from many sources of selective mortality during embryonic and early postnatal

stages and most selection on morphological traits probably operates during juvenile and adult stages". Many mammals and all primates clearly fall into this category, being characterised by high levels of maternal investment and sometimes also by substantial, although possibly collective and indirect, levels of paternal care.

Yet, however much flexibility can be demonstrated in the response of brain size to changes in adult body size, sexually mediated differences in brain weight are liable to be confounded by differences in overall body size in all sexually size dimorphic species, including man. This is a recurrent problem in all comparisons involving two or more organisms that differ in body size. It becomes crucial to distinguish between differences that reflect functional scaling to body size and grade effects that represent fundamental differences in biological adaptation. A simple expedient for excluding scaling effects is to focus on species of the same body size (see also Martin, 1982) and this procedure has been adopted in comparing the brain weights of males and females of monomorphic primate species. These data are particularly suitable since, for males and females drawn from the same species and having the same body size, intersexual differences in brain size can incontrovertibly be ascribed to a genuine degree of sexual dimorphism in the brain.

Brain weights of females were plotted against those of

males for 18 monomorphic primate species (see Figure 5.5). The results were remarkable in that for the larger simian species, with body weights in excess of 5,000g, the average female brain weight was consistently lower than that of the conspecific male whereas, for those species with adult body weights less than 4,000g, including five prosimians, there were virtually no differences in brain weight according to sex. This strange dichotomy calls for some explanation. Moreover, at least five of the larger species share the same mating system - they are monogamous and thus exemplify the ultimate degree of shared parental investment. Apart from primary sexual function, male and female roles tend to converge in all their aspects; there is no identifiable link between these animals' sex and their commitment to any form of specialised activity which might make specific demands and call for a measured degree of adaptive response, differentiated according to sex. Yet it is precisely within these larger, monogamous species that male brain weights exceed those of females in contrast to the sexually undifferentiated brain weights of smaller individuals. An attempt will later be made to account for this apparent contradiction in terms of an evolutionary approach to the possible ontogeny of sexual dimorphism in overall body size (see pages 216-217). At present, it should merely be noted that there is evidence of sexual dimorphism in the adult brain sizes of males and females from the same species and with the same overall body size.



SOLID LINE DENOTES EQUIVALENCE OF MALE AND FEMALE BRAIN WEIGHTS

Female brain weight vs. male brain weight for monomorphic species

5.3 SEX DIFFERENCES IN THE ORGANISATION OF THE BRAIN

An element of sexual dimorphism in the organisation of the brain has been adduced in studies of man, primates and other mammals. In 1968, Dörner and Staudt reported a hormonally regulated sexual dimorphism in cell nuclear size in hypothalamic areas of the rat brain. The same workers (Staudt and Dörner, 1976) subsequently found a further sexual dimorphism in cell nuclear size in the central and amygdala regions, also under the neonatal influence of sex hormones.

Both Carter and Greenough, with their associates, chose to study golden hamsters, on account of their minimal dimorphism in body weight (Carter et al., 1972; Greenough, 1977). They found that this monomorphism extended to brain dimensions, which is in harmony with the findings of the present study. Males and females of small-bodied monomorphic primates, in the same weight range as hamsters, appear to share a common brain weight (Figure 5.5). However, when Greenough and his colleagues used Golgi staining techniques, it became apparent that, despite the absence of sexual size dimorphism, the brains of male and female hamsters were not identical. It emerged that, in the dorsomedial preoptic area, male dendrites were centrally concentrated with a more peripheral distribution of neuron dendrites in females. These patterns were found to persist among animals that had been subjected to neonatal hormonal manipulation,

although the treated females became more malelike and the castrated males more femalelike. Four possible explanations for these dimorphisms were proposed: differential growth rates, triggered formation of connections, directed growth and selective preservation. Goy and McEwen (1980) refused to choose between these possibilities on the basis of the available data, believing this to be inconclusive. Moreover, the alternatives need not be mutually exclusive and differential growth is an attractive candidate, at least as a contributory factor, since it so often promotes other aspects of evolutionary change.

There is also firm evidence of sexual dimorphism in the rat brain. Gorski et al. (1977, 1978) found so striking a dimorphism in the medial preoptic area of the brains of adult Sprague Dawley rats that it was possible to discriminate male from female accurately on the basis of slides including this brain area alone. Tehrani et al., (1984) also reported sexual dimorphism in the rat brain and attributed this to differential exposure to sex steroids in perinatal life. They identified a 'basal' female state and found significant differences between the number, affinity and specificity of high affinity dopamine binding sites in normal male and female rats.

Using data generated by the Neuropsychology Unit, London, Canada, McGlone (1984) contrasted the effects of

unilateral lesions on both speech and spatial task competence in right-handed men and women. She concluded that "the cerebral representation of cognitive abilities was more heterogeneous in females than males. Specifically, the male brain may be more asymmetrically organised than the female". She also remarked that both anterior and posterior regions of the left hemisphere seemed to be critical speech zones in men, whereas in women only anterior lesions produced aphasia. These observations were explained in terms of sexual differences in the intrahemispheric organisation of speech and McGlone also inferred sex-related intrahemispheric differences in the performance of spatial tasks.

Kolb and Wishaw (1985) have challenged McGlone's view that intersexual differences in cognitive ability, following trauma, can be attributed to greater symmetry in the female brain than in the male brain, dismissing this explanation as an over-simplification. They cited the work of Inglis and Lawson (1981, 1982), which indicated that left hemisphere lesions are equally disruptive in males and females, and noted that several other researchers have found no sex differences in the incidence of a variety of symptoms commonly associated with damage to the right hemisphere. Kimura (1983) showed that the pattern of cerebral organisation <u>within</u> each hemisphere may differ between the sexes (in harmony with the findings already quoted for hamsters and rats). Both Bryden (1982) and Kolb

and Wishaw (1985) blame procedural differences, small sample sizes and great variability for some of the inconsistencies that characterise the literature on sex-related differences in lateralisation. They further remark that, although the available data from neurological patients suggests that unilateral lesions have different effects in males than in females, this is not, in itself, sufficient to establish precisely how the sexes differ in cerebral organisation.

In 1976, Witelson studied spatial processing in 200 normal boys and girls between 6 and 13 years of age. She found that boys performed in a manner consistent with right hemisphere specialisation by the age of 6 years, suggesting that sexual dimorphism in the neural organisation underlying cognition was already developed in these young children. Kolb and Wishaw (1985) also reported evidence from normal, healthy adults for at least four significant sex-related cognitive differences: Verbal differences, visuospatial differences, differences in mathematical ability and differences in aggression. They concluded that these were "at least partly due to neurological factors that may be modulated by the environment".

Apart from differences in male and female responses to traumatic incidents, many diseases, including epilepsy and infantile autism, show sex-related patterns. Taylor

(1985) highlighted the occurrence of a consistent sex-bias in three independent series of patients with temporal lobe epilepsy (Taylor and Falconer, 1968; Taylor, 1972 and Ounsted et al., 1966), although the investigations took place in different towns, covered different age groups, and each study comprised at least three aetiological groups. The sex-related nature of the findings appeared to be invariant and, since epilepsy is essentially a disease of the brain, the consistent general bias towards males as sufferers from the condition points to a degree of sexual dimorphism in the organisation of the brain. Indeed, the extra risk of epilepsy in males persists over time and place (Taylor, 1985) and is further corroborated by Sillanpää's epidemiological data of 1973, with its male prevalence of 3.6/1000 and female prevalence of 2.8/1000 (Sillanpää, 1973). These results were based on a sample of 108,019 subjects under the age of sixteen, which included 348 epileptics. The present author's further analysis of this subset yielded a statistically significant difference between the proportion of males and females affected by the disease (Chi-squared = 5.39, d.f. = 1, $p < 0.05$). Taylor (1985) further suggested that "different rates of development obtained between both the sexes and the hemispheres". The writer's own examination of Taylor's (1969) data failed to support this claim, which appears to have been based on visual impression rather than rigorous examination. Indeed, Taylor cites his inference as deriving from "an analysis by side and sex of

the age-of-onset histograms". However, Taylor's 'histograms' are misleading because they have not been standardised for differences between the sample sizes for males and females. A formal statistical analysis of Taylor's data, using a procedure due to Smirnov (see Conover, 1980, page 368 et seq.) yielded a significant association between age-of-onset and hemisphere (Dmax = 0.31; $p < 0.05$) but failed to indicate any significant interaction between age-of-onset and sex. This is perhaps hardly surprising in view of the small sample sizes employed. At the same time, findings of sexual dimorphism in the nature of the epileptic aura, the brief period of precognisance before some fits, indicate that there may well be sexually mediated differences in the organisation of the human brain (Taylor, 1981; Remillard, 1982).

Kolb and Wishaw (1985) focused on maturation rate and environment as key factors in shaping the behaviour of males and females, from infancy through to adulthood. Even at birth, females are generally more mature than males (see page 140 and Tanner, 1960) and developmental studies suggest that this feature also extends to cerebral maturation (Kolb and Wishaw, 1985). Indeed, Waber (1984) suggests that, in man, it is by exploiting an initially greater potential for cognitive responses that the female infant develops enhanced social skills, engaging in early interactions with other individuals while the male infant

is better endowed to develop tactile and spatial skills. These early infantile experiments could then, according to Waber, lead to sexually divergent choices of strategy in common situations. If early differences in the brain are further reinforced by the behavioural tendencies they generate, then a continued differentiation of the brain along sexual lines would ensue.

However, it is important to distinguish between speculation and hypothesis and it is beyond the scope of the present study to evaluate Waber's proposition. Nevertheless, it is well known that girls typically acquire linguistic skills ahead of boys, both reading and writing better as well as employing much richer vocabularies than boys at any given age. Moreover, despite some anomalies, tachistoscopic and dichotic studies frequently indicate an earlier evolution of brain asymmetry in boys than in girls. For instance, Witelson (1976) found that boys between the ages of 6 and 13 years obtained higher left hand scores than right hand scores whereas there was no such difference in handedness among girls of the same age. Kolb and Wishaw (1985) proposed that, in keeping with females attaining physical maturity at an earlier age than males, it is most likely that the male brain matures more slowly than the female brain. Since maturation rate is regarded as a critical determinant of brain asymmetry, then the more slowly a child matures, the greater the ensuing degree of cerebral

asymmetry. Waber's (1976) study of cognition as a function of maturation vindicates this interpretation. She found that, regardless of sex, early maturing adolescents performed better on tests of verbal as opposed to spatial abilities, whereas the reverse was true for late maturing subjects.

Bleier et al., (1986) have cautioned against the assumption of gender related differences in cognitive function on the basis of poorly designed experiments lacking adequate control. They condemn defects in the psychological instruments designed to test 'spatial ability' and question whether it is a legitimate, unitary construct. They further remark that, even when found, gender-related differences account for no more than 1%-5% of the population variance and are of relatively small magnitude - the difference between mean scores is only one-quarter to one-half of a standard deviation.

As well as the inconclusive nature of some of the evidence for differences in cognitive functioning between males and females, there is no certainty that a correlation exists between visuo-spatial ability and hemispheric lateralisation. Yet several of the studies reported above suggest that there are real differences in cerebral organisation between males and females, in species as diverse as rats, hamsters and man (e.g., rats: Gorski et al., 1977, 1978; hamsters: Carter et al., 1972;

Greenough et al., 1977; humans: Witelson, 1976; Kolb and Wishaw, 1985). These may comprise differences between the sexes in cerebral organisation within hemisphere, together with differences in lateralisation between hemispheres. It seems that some research has foundered when attempting to use these results as a basis for inferring behavioural and cognitive differences.

It might be expected that differences in lateralisation between males and females would be accompanied by sexual dimorphism in the corpus callosum, the main 'bridge' between the hemispheres. This was duly investigated and, in 1982, De Lacoste-Utamsing and Holloway reported a "striking" sexual dimorphism in the shape and surface area of the human corpus callosum. This was determined from post-mortem examinations of 14 normal adult brains, 9 male and 5 female. The female splenium was reported as both more bulbous and larger than the male counterpart and "gender differences in the degree of lateralisation for visuo-spatial functions" were consequently inferred. In a subsequent extension study based on a new sample (Holloway and De Lacoste-Utamsing, 1986), 16 human brains (8 male and 8 female) were examined, with the two authors working independently of each other and using different methods. The results replicated the findings of the earlier work and were taken to vindicate the previous conclusions, including those relating to gender differences in cognitive task behaviour.

However, these studies have drawn extensive criticism, not least because the combined sample for the two investigations comprised only 17 male and 13 female brains. Moreover, they were concerned with a structure characterised by considerable individual variation in both size and shape, irrespective of gender (Bleier et al., 1986). De Lacoste-Utamsing and Holloway's results do not appear to have been replicated satisfactorily by subsequent workers (including Witelson, 1985; Demeter et al., 1985; Juraska, 1985; Bleier et al., 1986; Oppenheim et al., 1987). Bell and Variend (1986) similarly found no evidence of sexual dimorphism in the corpus callosum during childhood. Oppenheim et al. (1987) used an in vivo technique, which enabled them to compare the dimensions of the corpus callosum in a much larger sample of 40 male and 40 female subjects. The callosal measurements they derived from morphometric analysis of magnetic resonance image scans yielded no significant sex-related differences for callosal areas, maximum callosal width or callosal curvature. In addition, an impartial observer failed to match the success described by De Lacoste-Utamsing and Holloway (1982) in correctly categorising callosal outlines as male or female on the basis of their morphology. Bleier et al. (1986) also found it impossible to predict gender from the size or shape of any individual corpus callosum. It seems likely that De Lacoste-Utamsing and Holloway were misled by the specific attributes of the

particular small sample they studied. Indeed, as highlighted by Bleier and her collaborators, they undertook their study after fortuitously noticing a sex difference in the shape of the splenium in a series of brains they were examining. In such a circumstance, the existence of a sexual dimorphism cannot be tested properly without recourse to a new, independent sample, collected with due control and knowledge of all possibly relevant variables, such as age or cause of death.

Bleier et al. (1986) have suggested that, although the mechanisms are as yet obscure, the specific patterns of callosal connections are shaped partly by sensory, and perhaps motor, experience. They note that, at birth, callosal connections are distributed uniformly across the visual, auditory and somatosensory cortex in kittens and rodents, unlike the mosaic pattern of distribution typical in adults. The work of Juraska and her associates supports this proposition. They found significantly larger middle and posterior thirds of the corpus callosum in rats reared in a complex environment compared with rats reared in isolation (Juraska, 1985; Juraska and Meyer, 1985; Juraska et al., 1985).

The brief history of research into sex-related differences in the corpus callosum illustrates the dangers of making sweeping generalisations based on small, and possibly biased samples. Nevertheless, although flawed by

methodological defects, De Lacoste-Utamsing and Holloway's work served as a catalyst for much subsequent research. Indeed, recalling the Birmingham study of sexual dimorphism in human birth weights (Gibson and Mckeown, 1952), it may be that even larger samples than those employed by Oppenheim et al. (1987) will, after all, reveal a degree of sexual dimorphism in the corpus callosum. However, aside from this, two key questions remain: Whether a direct relation exists between the size of the splenium and the degree of symmetry of hemispheric functioning and, if so, whether a larger splenium would necessarily reflect less hemispheric specialisation for visuospatial functions. Bleier et al. (1986) caution against assuming the existence of these relations in the absence of adequate evidence. They are not satisfied that "our existing knowledge of the corpus callosum and of the cortical functions its axons subserve permits interpretations relating differing cognitive functions to variations in size and shape of the callosum".

Nevertheless, despite the uncertainties and controversies, the available data attest to a degree of sexual dimorphism in the brain, already discernible in immature individuals and persisting into adulthood. The record of sexually different responses to disease in humans as well as differences in the developmental patterns of boys and girls, when taken in conjunction with pathological data obtained from rats and hamsters, suggest

that there are real, if imperfectly understood, differences between the organisation of the brain in male and female mammals.

5.4 ADULT BODY SIZE DIMORPHISM AND RELATIVE BRAIN SIZE

The approach presented below was developed from considerations of well-known allometric relations linking brain weight and body weight at various taxonomic levels. It is clear from numerous previous publications (e.g., Gould, 1966; Jerison, 1973; Martin, 1981), as well as from analyses carried out in the context of the current study, that a best-fit line for brain size against body size for a large sample of mammal species exhibits a quite high slope value. Indeed, there is some indication that for placental mammals generally this slope value approximates to 0.75 (Martin, 1981). It has also been known for some time that lower slope values are found when smaller taxonomic units are examined (e.g. families, subfamilies or genera) and that the lowest values of all occur when best-fit lines are determined from brain:body size relationships among adults within a species (Martin and Harvey, 1985). As an explanation of this phenomenon it has been suggested that, within species and during the early stages of divergence between species, selection initially operates on body size, such that brain size is only passively affected by its developmental link with body size (Lande, 1979, 1985). More recently, Pagel and Harvey (1988) have challenged this interpretation and

demonstrated, with a simulation study, that "the regular increase in slope with taxonomic level emerges as a consequence of error variability patterns alone regardless of which technique is used to analyse the data". Nevertheless, significant phenotypic correlations persist between adult brain and body weights, even within species, for most mammals except primates. These are consistent with quite high genetic correlations between the same characters, such as those estimated for mice and rats (Roderick et al., 1976; Atchley, 1984; Atchley et al., 1984; Lande and Arnold, 1984).

Primates, however, diverge from this general trend (Jerison, 1973; Holloway, 1980; Lande, 1985; Martin and Harvey, 1985), showing a much lower average phenotypic correlation between within species adult brain and body weights, calculated separately for males and females. Assuming comparable genetic and phenotypic correlations, as for other mammals, this suggests a rather weak coupling of body and brain size in primates. In consequence of this somewhat loose genetic link (see also page 171 et seq.), it is quite feasible for a change in adult body size to have little effect on brain size over relatively short periods of evolutionary time. Besides, there is good evidence that closely related primate species of differing adult body size may fit common ontogenetic trajectories, as is the case (for instance) with chimpanzees and gorillas (Shea 1981, 1983). The subsequent divergence in

adult body size appears to result primarily from continued growth after the developmental stage at which the brain has already more or less attained its target size.

A similar situation obtains in the ontogeny of sexual dimorphism in overall adult body size, with males and females following a common growth trajectory during early life, beyond the stage at which brain growth has virtually ceased. Holt et al. (1975) have shown that during fetal life (and even longer for Homo sapiens), brain weight increases isometrically with body weight for primate species as diverse as man, chimpanzee, macaque and Presbytis (see Figure 5.2). Subsequently, perhaps following the attainment of a critical size or age, the rate of increase in body size dramatically outstrips that of the brain. It is the timing of this break with the initial shared phase of isometry in body and brain growth that differentiates between the various primate species. Holt and his colleagues reported the chronology of the point of departure as "prior to birth for Semnopithecus (Presbytis), approximately 150 days gestation for the macaque, just after birth for the chimpanzee, and about two years of age postnatally for the human". The brain weight for each individual species then diverges from the common trend and moves towards its own ultimate value. An allometric plot, based on prenatal data for 25 humans and 47 macaques, demonstrates the remarkably "close, if not identical, relationship that exists between macaque and

man when brain weight is plotted against body weight during fetal life" (Holt et al., 1975).

However, even a very close allometric correspondence can mask important differences between man and non-human primates. Martin (1983) examined the logarithmic plots of fetal brain weight against fetal body weight for 6 primate species (including man) and 10 non-primate species. He found a clear distinction between the best-fit lines (major axes) calculated separately for these two categories whereas the best-fit line for Homo sapiens coincided very closely with the general best-fit line for all primates. Nevertheless, and despite a general overlap in adult body size (57Kg for man; 30-100Kg for great apes) and comparable gestation periods (270 days for man; 245-270 days for great apes), Homo sapiens produces neonates of approximately twice the weights found for new-born gorillas, chimpanzees or orang-utans. This implies that human mothers devote a relatively greater input of energy and other resources to fetal brain and body development over a standard time than do any other of the great apes, man's nearest relatives. Prenatal growth in man appears to follow the typical primate brain:body trajectory, without significant deviation, but at a faster rate (Martin, 1983).

The overall impression is that within species and at low taxonomic levels brain:body size relations are likely

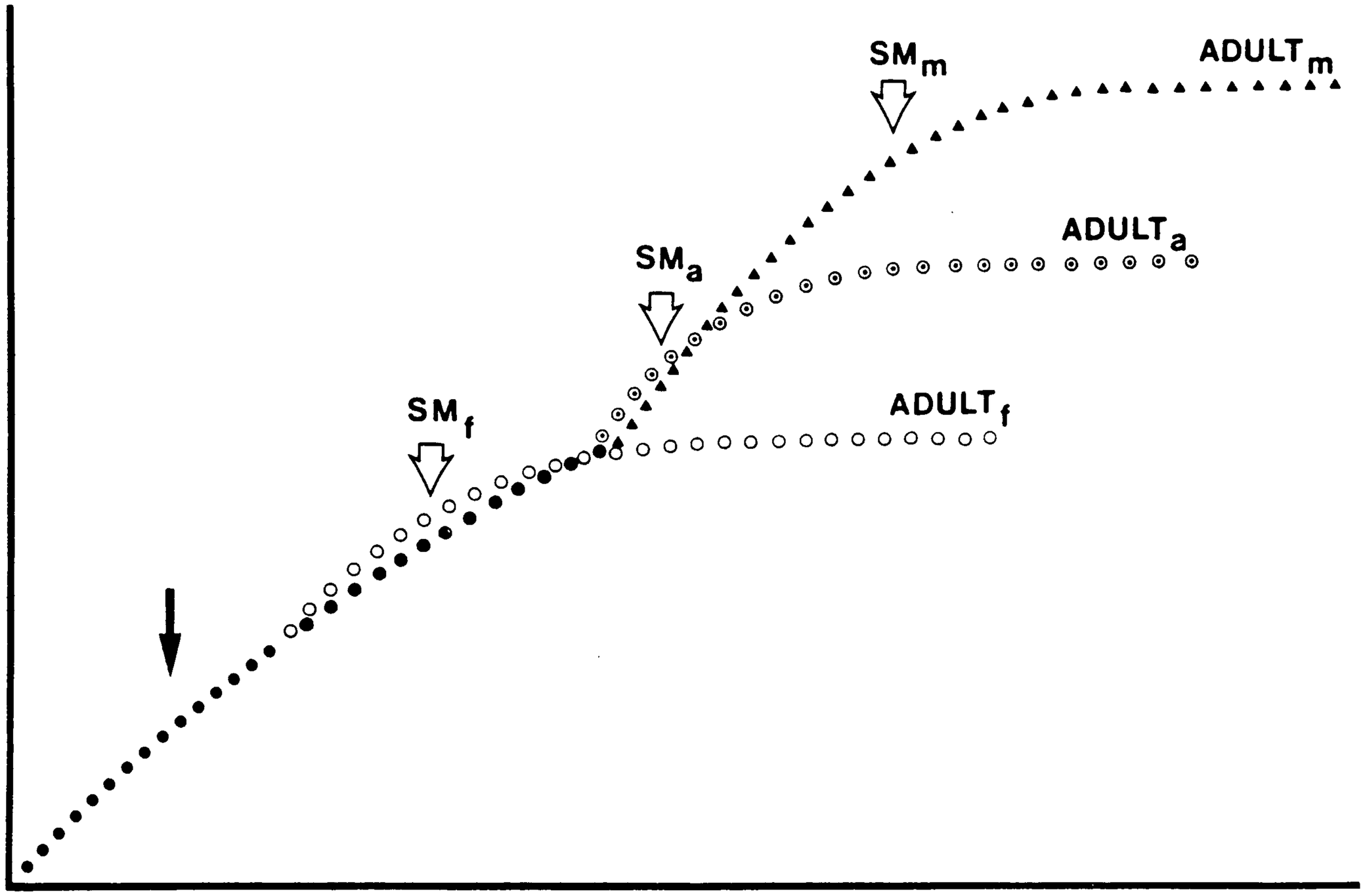
to reflect common ontogenetic trajectories (with correspondingly low slope values for allometric best-fit lines), whilst at higher taxonomic levels selection for brain size itself results in a shift towards higher slope values for plots of brain size against body size without the constraint of a common ontogenetic trajectory (Lande 1979, 1985; Martin and Harvey, 1985). The same considerations must surely apply to males and females of the same species, which have already been shown to share a common growth trajectory (see previous paragraph and Figures 4.1-4.4 & 5.1). Hence, in dimorphic species, it would be expected (and is abundantly confirmed by data presented below) that females should have higher relative brain sizes than males of the same species. This in itself would be a somewhat banal finding were it not for the more powerful implications inherent in intrasexual differences between logarithmic quotients of encephalisation of dimorphic and monomorphic species (the logarithmic quotient of encephalisation being defined as the Log EQ value or vertical displacement of a species' coordinates from the chosen line of best fit).

Most organs continue to grow, in harmony with changes in overall body size, from birth, through infancy and adolescence and until an individual has reached full adulthood. The brain is rather unusual in this respect since it develops rapidly during fetal and early postnatal life and then grows much more slowly to reach its adult

size well before the attainment of sexual maturity (see Figure 5.3). The present research utilises this attribute in order to breach the circularity inherent in most discussions of sexual size dimorphism. The specific consideration of brain size in relation to adult body size affords a special opportunity for investigating the direction of evolutionary change and assessing the relative merits of contradictory hypotheses by means of clearly defined and testable predictions. Teeth, although they do not share the brain's remarkable prenatal growth rate, also attain their adult size at an early stage in development, a feature which is exploited in Chapter 6.

The relevance of the unusually early completion of brain growth to analysing the origins of sexual size dimorphism can conveniently be illustrated (see Figure 5.6). It was assumed that there was a sexually monomorphic ancestral species with a single adult body size for both males and females (ADULTa) achieved along a common growth trajectory. It was further assumed that the age of attainment of sexual maturity for this ancestral species (SMa) was identical for males and females. The latter assumption seems reasonable in the light of the common age of sexual maturity recorded for both sexes of extant monomorphic species (see Figure 3.5). A <u>prima facia</u> case can also be made for the postulated monomorphic ancestor. In 1972 Crook based the following inference on his observations of the distribution of sexual dimorphism

FIGURE 5.6



See page 194 for definitions of terms

Diagram of growth processes leading to divergent male and female adult body weights.

(After Willner & Martin, 1985)

among primates: The fact that "extreme dimorphism is relatively infrequent in primates and is largely confined to Old World Anthropoidea indicates that marked morphological and behavioural dimorphism is not a primitive characteristic of primates but has evolved in certain genera in response to particular patterns of living". In addition, Young (1950) deduced from fossil evidence that small size was a "characteristic common to all earlier forms", whilst Römer's (1971) examination of fossil dental material led him to conclude that primitive eutherian mammals were "generally small creatures, averaging about the size of rats and mice". Even today, the majority of extant mammal species are small, again supporting the view that the ancestral stock was also small. Since small size tends to preclude body size dimorphism, especially with respect to smaller body size in females (see page 77), it seems unlikely that either mammals in general or primates in particular are descended from a dimorphic ancestor. From a hypothetical monomorphic ancestor, sexual dimorphism could arise in three possible ways:

1. Females achieve adulthood at a smaller adult body size (ADULTf) and achieve sexual maturity at an earlier age (SMf).
2. Males achieve adulthood at a larger adult body size (ADULTm) and attain sexual maturity at a later stage (SMm).

3. A combination of both developments occurs.

Thus far, all three possibilities are compatible with the allometric relations determined for each of brain size, age at sexual maturity and lifespan with body weight among those mammal species that have become sexually size dimorphic as adults. Moreover, each of the scenarios is consistent with the relative ages at which conspecific males and females attain sexual maturity (see Figure 3.5). There are, however, distinctive implications for brain:body size relationships which might permit a choice between the suggested alternatives. Since growth of the brain virtually ceases early in ontogeny, (see black arrow in Figure 5.6), earlier attainment of sexual maturity in females, at a correspondingly smaller adult body size, should lead to higher than expected encephalisation quotients for these females, in comparison with other females. Conversely, later attainment of sexual maturity in males, at larger adult body size, should result in lower than expected encephalisation quotients for these males, in comparison with other males.

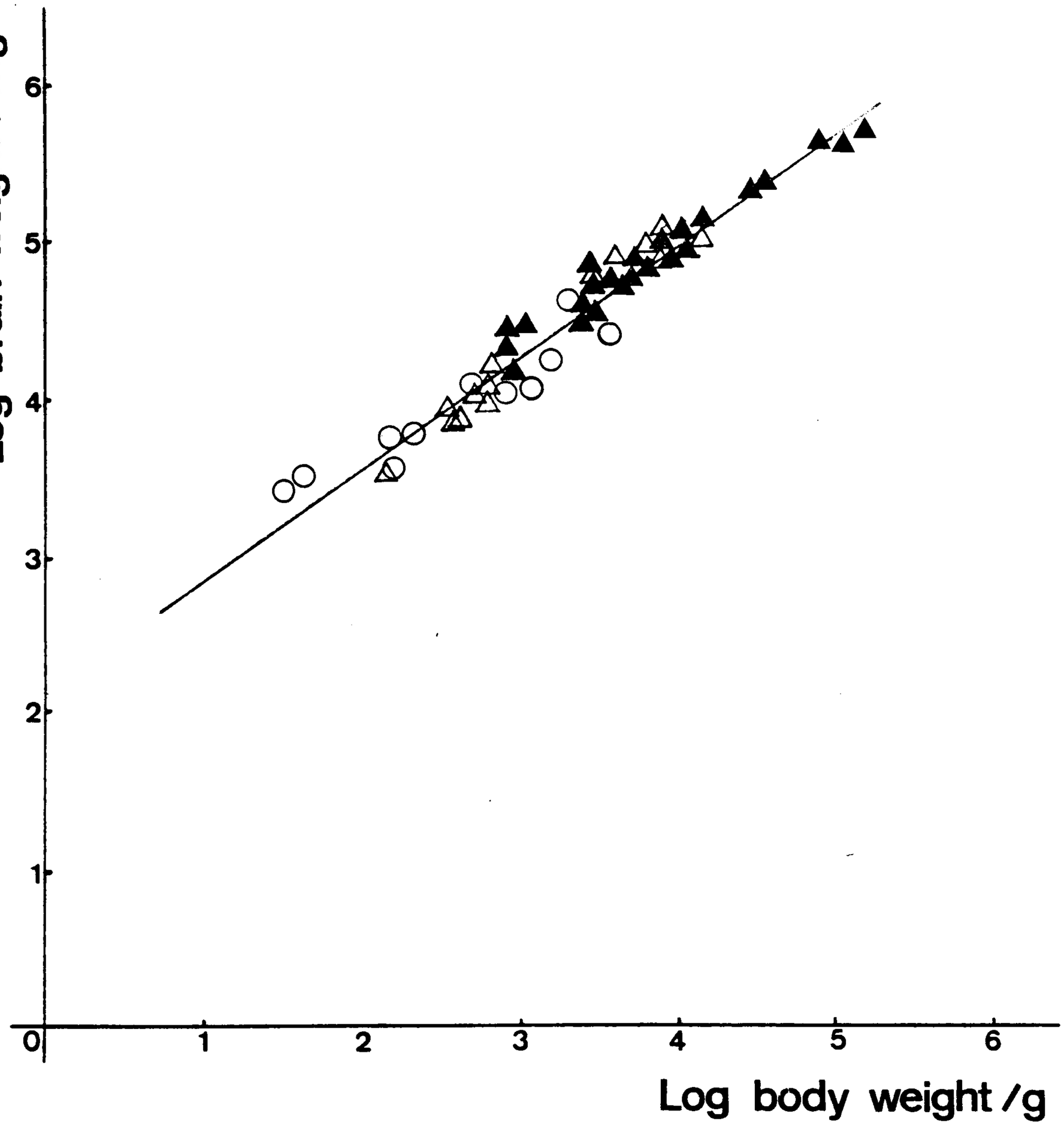
Naturally, over the long term, positive selection for an optimal brain size should counteract such initial effects resulting from ontogenetic processes. Nevertheless, the possibility remains that these effects would persist long enough, in evolutionary terms, to indicate how sexual dimorphism arose in at least some

individual cases. Comparing Log EQ values within sex and between dimorphic categories affords an opportunity for breaching the circularity so frequently inherent in dissertations on the evolutionary origins of sexual dimorphism in adult body size. Higher than expected Log EQ values for females of sexually dimorphic species would indicate evolutionary reduction in female body size, whereas lower than expected Log EQ values for males would indicate increase in male body size.

Problems of grade distinctions between groups of species have already been discussed. To avoid these complications, the analysis of brain to body weight ratios was restricted to data for simian primates. Monkeys and apes constitute a well defined grade in terms of relative brain weight, as evinced by the allometric plots of brain and body weights which show a marked upward shift of simian primates in relation to other non-primate mammal species (see Figure 3.1). The distinction between simian and prosimian primates is less obvious because of differences in the range of body sizes typically associated with the two groups (see Figure 5.7). However, many of these small animals are nocturnal and sufficiently divergent from simian primates in their patterns of behaviour to warrant recognition as a separate group.

The concept of grade is not restricted to purely allometric considerations and in examining a distinction

FIGURE 5.7



▲ dimorphic simian
△ monomorphic simian
○ prosimian

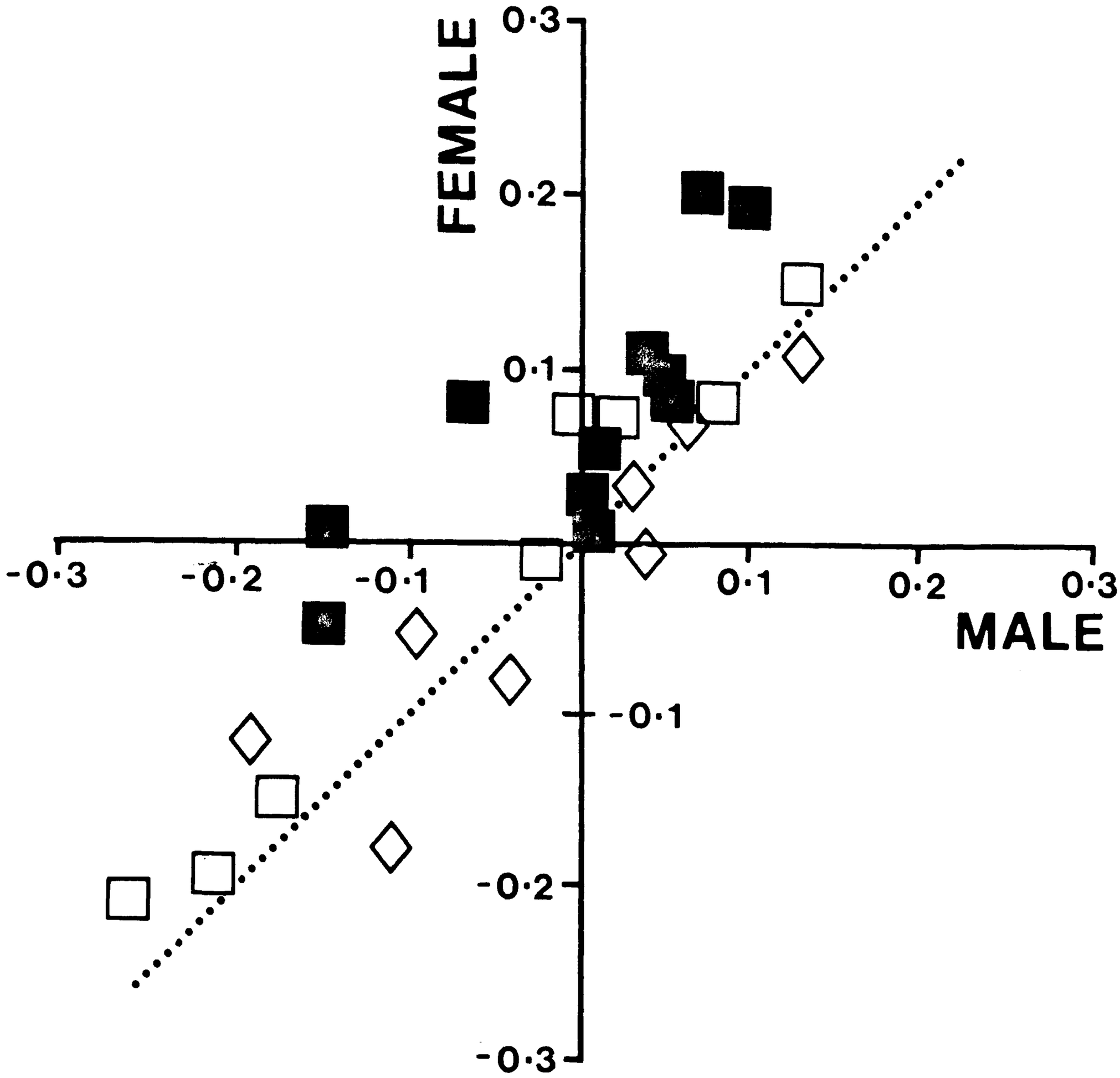
Logarithmic plot of brain weight against body weight for primates.

as subtle as sexual dimorphism, which reflects a refined difference in adaptation between individuals of the same species, it is preferable to err on the side of caution. Recalling the distinction between size-related scaling effects and those due to modification in biological function (see page 51), Figures 3.1 - 3.4 indicate that monkeys and apes together comprise a single evolutionary grade, differentiated not only in terms of brain weight, but also with respect to lifespan and the attainment of sexual maturity. Accordingly, in order to obtain an unbiased basis for comparisons between the sexes, it was necessary for the analyses to be carried out on data drawn from simian primate species alone.

However, it has also been reported that frugivores tend to have larger brains than folivores of the same body size (Harvey et al., 1987), so that there could still be a grade distinction, even within the restricted category of simian primates. To test this possibility, major axes were calculated for the logarithmic plots of brain weight against body weight for the complete sample of simian primates as well as for frugivorous species alone. Since the axes obtained did not differ significantly in respect of either gradient or intercept (b=0.717, a=2.206 for the complete sample and b=0.747, a=2.213 for frugivorous species alone), the use of a major axis based on the combined data set for frugivores and folivores of both sexes was vindicated. The Log EQ values were then

calculated for males and females of each species relative to the common major axis for an overall logarithmic plot of brain size against body size for the complete sample of simian primate species.

The results obtained fully endorsed the potential implications of Figure 5.6 regarding intersexual differences in Log EQ values. Females of dimorphic species generally had greater Log EQ values than males of the same species, whereas in monomorphic species there was no such trend, with males actually tending to have slightly or markedly higher Log EQ values than females (see Figure 5.8). Since males are consistently the larger sex among those primate species which show any marked degree of dimorphism, the direction of the enhanced Log EQ values favoured females. Although it is beyond the scope of the present research to investigate the respective male and female Log EQ values for non-primate species with the female the larger sex, it is predicted that among such individuals the Log EQ values would be greater for males. In general, a higher Log EQ value would be associated with the smaller-bodied sex as compared with the opposite sex. Besides, and as expected, data of the current study indicated that the differences between Log EQ values of males and females were most pronounced in species with marked sexual dimorphism (male:female body weight ratio greater than 1.3) as compared with species exhibiting only mild sexual dimorphism (see Tables 5.2 and 5.3).



DOTTED LINE DENOTES EQUIVALENCE OF MALE AND FEMALE LOG EQ VALUES

■ STRONGLY DIMORPHIC SPECIES

□ MILDLY DIMORPHIC SPECIES

◇ MONOMORPHIC SPECIES

Log EQ values for female simian primates against those of conspecific males

(After Willner & Martin, 1985)

TABLE 5.2

DIFFERENCES BETWEEN FEMALE AND MALE LOG EQ VALUES
CALCULATED FROM THE COMMON MAJOR AXIS

SPECIES	LOG EQ MALE (A)	LOG EQ FEMALE (B)	(B)-(A)	D
MONOMORPHIC: D < 1.15				
Aotus trivirgatus	0.029	0.021	0.008	1.03
Ateles fusiceps	0.035	-0.011	-0.046	0.97
Ateles geoffroyi	0.068	0.029	-0.039	0.98
Ateles paniscus	-0.016	-0.021	-0.005	1.06
Callithrix jacchus	-0.093	-0.067	0.026	1.01
Hylobates Agilis	0.057	0.052	-0.005	1.07
Hylobates lar	0.120	0.086	-0.034	1.03
Hylobates moloch	0.063	0.071	0.008	1.05
Saguinas geoffroyi	-0.052	-0.105	-0.053	0.98
Saguinas oedipus	-0.112	-0.106	-0.089	0.96
Symphalangus syndactylus	0.016	0.022	0.006	1.05
Tarsius syrichta	*	-0.180	*	1.07
MILDLY DIMORPHIC: D =< 1.3				
Alouatta palliata	-0.221	-0.195	0.026	1.26
Colobus badius	*	-0.078	*	1.15
Colobus guereza	*	*	-0.144	1.24
Lagothrix lagotricha	*	*	0.045	1.20
Macaca arctoides	-0.069	-0.026	0.043	1.18
Macaca mulatta	0.020	0.043	0.023	1.17
Miopithecus talapoin	*	0.179	*	1.23
Pan troglodytes	0.107	0.123	0.016	1.23
Papio papio	0.011	0.059	0.048	1.18
Presbytis Cristata	-0.083	-0.088	-0.005	1.19
Presbytis obscura	-0.174	-0.158	0.016	1.22
Saimiri oerstedii	*	0.136	*	1.21
Saimiri sciureus	0.103	0.116	0.013	1.15

continued....

TABLE 5.2 continued

SPECIES	LOG EQ MALE (A)	LOG EQ FEMALE (B)	(B)-(A)	D
STRONGLY DIMORPHIC: D > 1.3				
Cebus albifrons	0.210	0.200	-0.010	1.41
Cebus apella	0.123	0.200	-0.077	1.49
Cebus capucinus	0.124	0.204	0.080	1.33
Cercocebus albigena	0.030	0.049	0.019	1.37
Cercocebus galeritus	-0.007	0.062	0.069	1.86
Cercocebus torquatus	-0.051	0.111	0.162	1.82
Cercopithecus aethiops	-0.016	0.034	0.050	1.41
Cercopithecus ascanius	0.031	0.094	0.063	1.45
Cercopithecus l'hoesti	-0.056	0.087	0.143	1.81
Cercopithecus mitis	-0.079	-0.058	0.021	1.72
Cercopithecus mona	0.022	0.150	0.128	1.76
Cercopithecus nictitans	-0.070	*	*	1.56
Cercopithecus pygerythrus	-0.020	0.116	0.136	1.78
Colobus polykomos	*	-0.069	*	1.44
Cynopithecus Niger	0.108	0.156	0.048	1.35
Erythrocebus patas	-0.075	0.068	0.143	1.99
Gorilla gorilla	-0.181	0.081	0.100	1.69
Macaca fascicularis	-0.037	0.035	0.072	1.52
Macaca maurus	-0.001	*	*	1.30
Macaca nemestrina	*	0.149	*	1.79
Mandrillus leucophaeus	*	0.071	*	2.53
Mandrillus sphinx	-0.058	*	*	1.90
Papio cynocephalus	-0.059	0.096	0.155	1.88
Papio hamadryas	-0.031	0.080	0.111	1.80
Papio ursinus	-0.145	0.020	0.165	1.94
Presbytis entellus	-0.124	*	*	1.46
Pygathrix nemaeus	-0.247	*	*	1.33
Pongo Pygmaea	0.025	0.112	0.087	1.98
Theropithecus gelada	-0.199	-0.045	0.154	1.66

MEANS & STANDARD ERRORS:	MALES (A)		FEMALES (B)	
MONOMORPHIC	0.0050±0.0218	(11)	-0.0346±0.0221	(14)
MILDLY DIMORPHIC	-0.0383±0.0426	(8)	0.0009±0.0344	(13)
STRONGLY DIMORPHIC	-0.0343±0.0212	(26)	0.0719±0.0170	(24)
ALL DIMORPHIC	-0.0359±0.0182	(34)	0.0470±0.0170	(37)

TABLE 5.3

INTERSEXUAL AND INTRASEXUAL DIFFERENCES IN MEAN LOG EQ VALUES ACCORDING TO DEGREE OF SEXUAL SIZE DIMORPHISM

1) INTERSEXUAL DIFFERENCES : PAIRED t-TESTS

	MEAN DIFFERENCE	t	n	p
MONOMORPHIC: D < 1.15	-0.0203	-1.95	(12)	n.s.
MILDLY DIMORPHIC: D =< 1.3	0.0225	3.75	(9)	<0.005
STRONGLY DIMORPHIC: D > 1.3	0.0875	6.29	(22)	<0.0005

2) INTRASEXUAL DIFFERENCES (FEMALES)

(COMPARISONS BETWEEN GROUP MEAN LOG EQ VALUES)

	t	n	p
MONOMORPHIC vs. MILDLY DIMORPHIC	0.88	(27)	n.s.
MONOMORPHIC vs. STRONGLY DIMORPHIC	3.81	(38)	<0.025
MONOMORPHIC vs. ALL DIMORPHIC	2.64	(51)	<0.01

3) INTRASEXUAL DIFFERENCES (MALES)

(COMPARISONS BETWEEN GROUP MEAN LOG EQ VALUES)

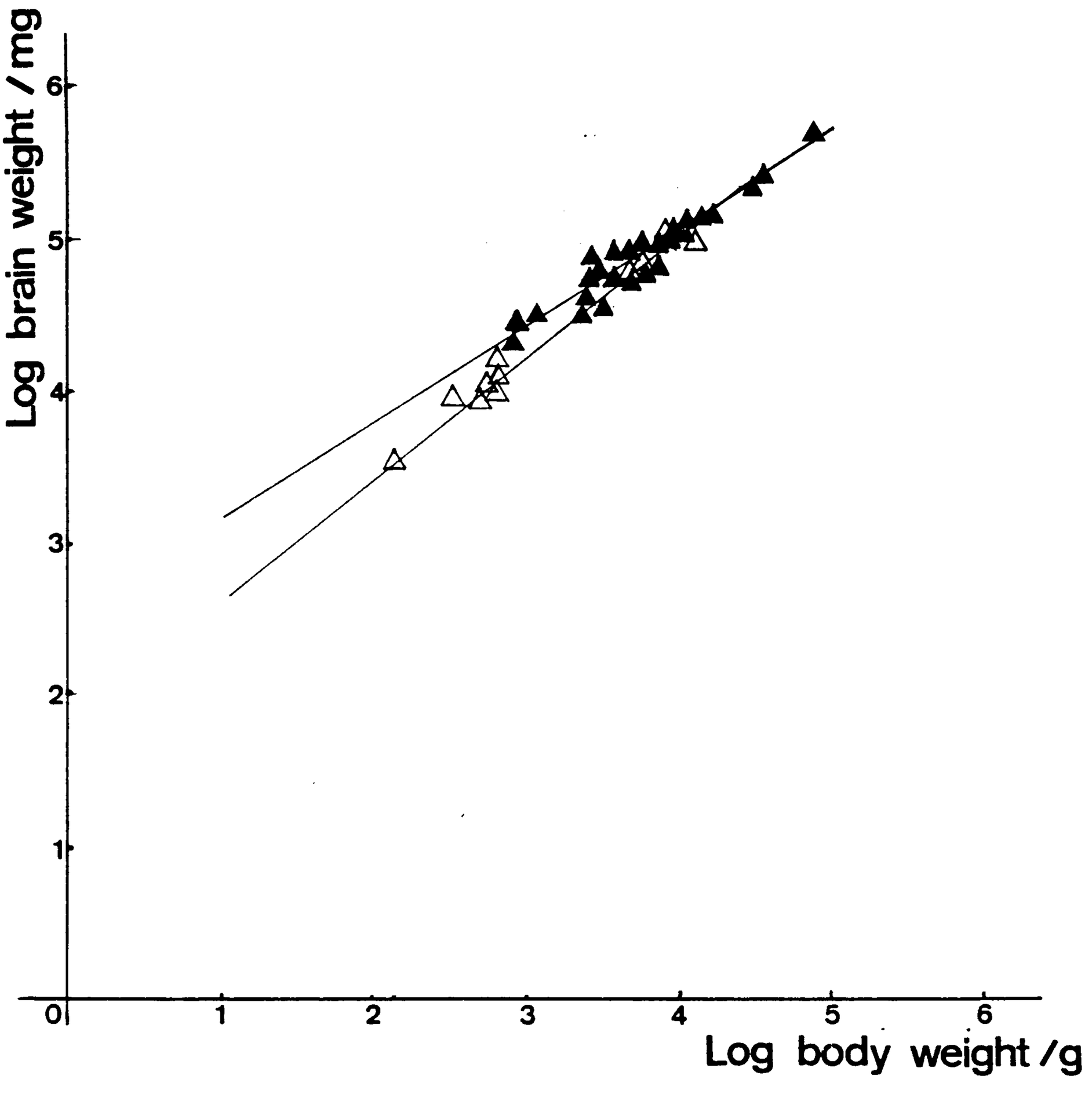
No significant differences were found between any classes of males.

Student t-tests based on the group means yielded no significant difference between male and female Log EQ values for monomorphic species whilst the difference for dimorphic species attained a significance level of $p < 0.05$. Subdividing the dimorphic group into two sub-classes of strongly and mildly dimorphic species, the group means for males and females of the first category differed at a significance level of $p < 0.0005$, whereas for the second category the difference in the intersexual group means failed to attain significance. In view of the relatively small sample sizes (males of 10 species and females of 14 species) and the considerable variability within these two groups it is not surprising that this lesser difference failed to reach statistical significance; the standard errors of the means for both mildly dimorphic classes (i.e., for both males and females), were more than double those of any other category.

In order to offset the variation <u>within</u> groups, paired t-tests were carried out on the differences between female and male Log EQ values within species. Once again, no significant differences were found between males and females of monomorphic species, but now the differences in Log EQ values between males and females of only mildly dimorphic species were highly significant ($p < 0.005$) and those of strongly dimorphic species were significant to an even greater extent ($p < 0.0005$).

Nevertheless, these findings only confirm that there are persistent Log EQ differences between males and females of sexually dimorphic species which are explicable in terms of the ontogenetic pattern of brain:body relationships and that these are, for the same reasons, characteristically absent in monomorphic species (see Figure 5.8). The results do not, in themselves, indicate the direction of body change involved. However, it is also found that females of sexually dimorphic simian primate species generally have higher Log EQ values than females of monomorphic species, a tendency which is most pronounced among the smaller bodied genera (see Figure 5.9). Now this might be attributed to selection for larger brain size in dimorphic species generally; but, since there is no marked tendency for males of dimorphic species to exhibit higher Log EQ values than males of monomorphic species (Figure 5.10), it would then leave unexplained an apparently differential selection for enlarged brain size between males and females of the same species. An alternative and more plausible explanation might be that the higher Log EQ values reflect a general trend to reduction in female body size in dimorphic species, with an accompanying increase in Log EQ generated by the ontogenetic effects outlined above. This effect has then been countered to some extent, although not entirely annulled, by selection for overall size increase in the larger-bodied species.

FIGURE 5.9

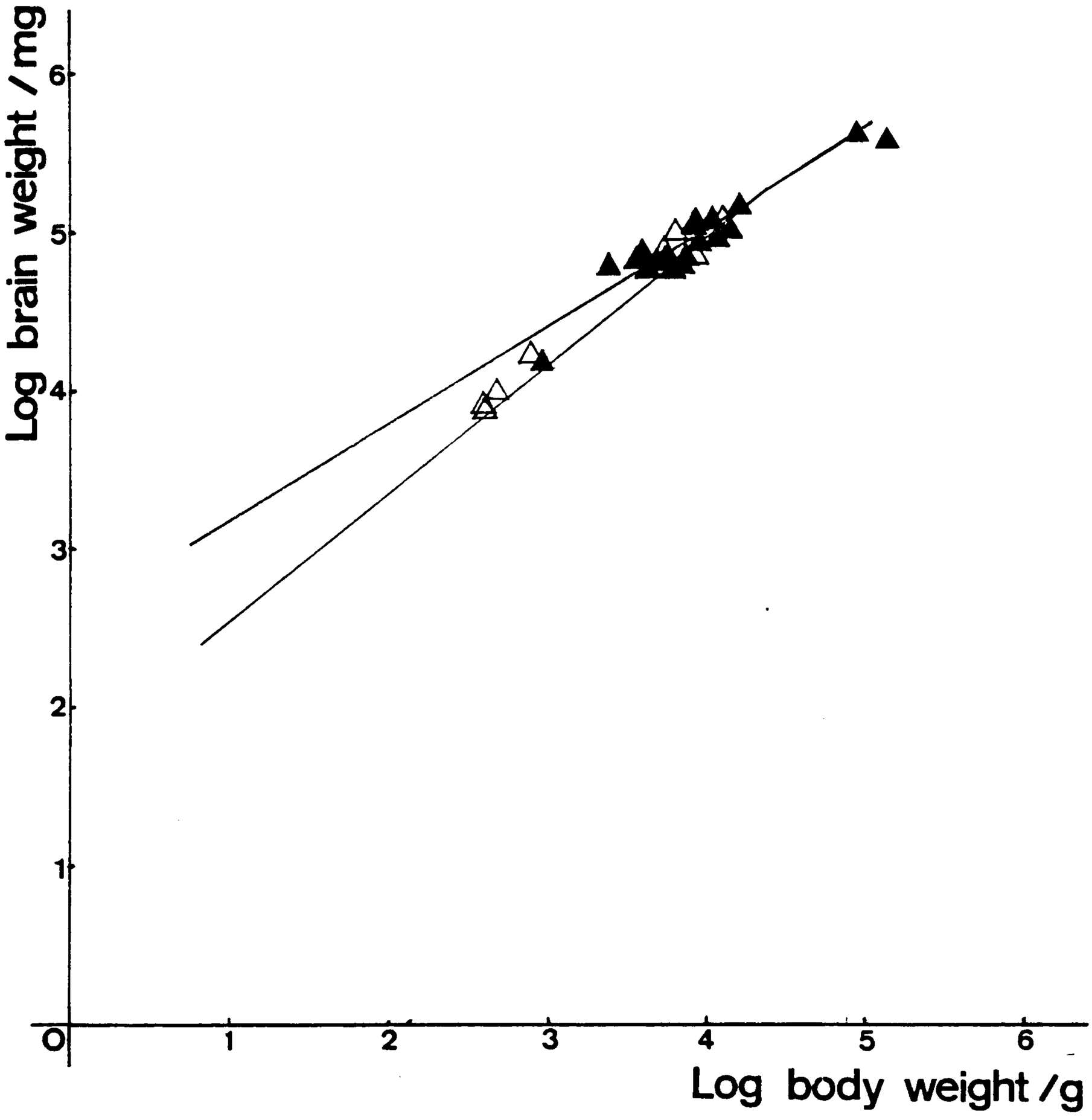


▲ dimorphic simian

△ monomorphic simian

Logarithmic plot of brain weight against body weight for female simian primates.

FIGURE 5.10

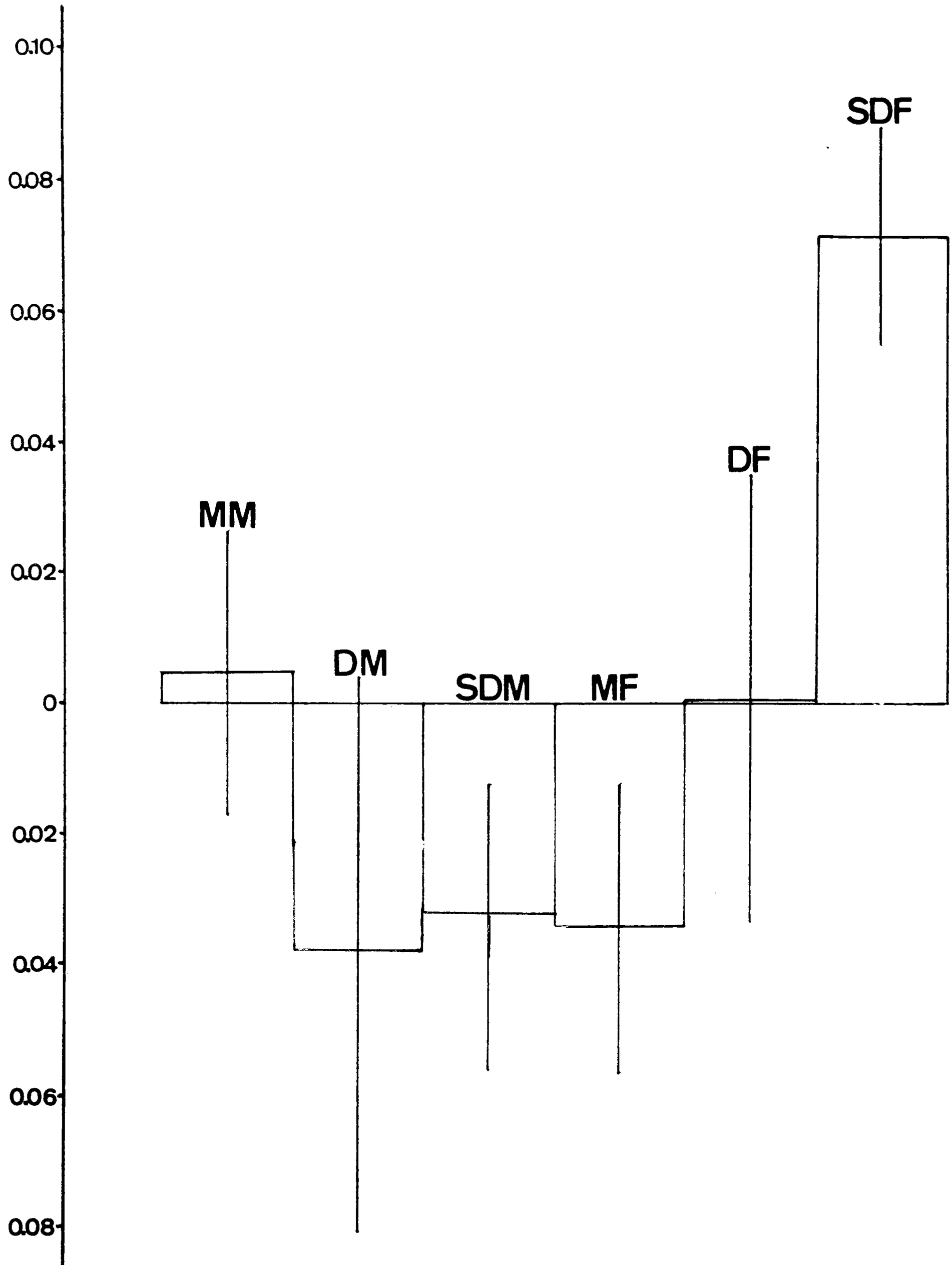


▲ dimorphic simian
△ monomorphic simian

Logarithmic plot of brain weight against body weight for male simian primates.

It is possible to assess the relative merits of these two explanations by examining the relation between the logarithms of brain weight and body weight among male simian primates (see Figure 5.10). It emerges that males of small-bodied dimorphic species also have slightly higher than expected Log EQ values compared to the common trend, but the effect is not as pronounced as with females. Although slight, this general tendency is consistent and the implications are discussed below (see page 208 et seq.). A plot of the mean logarithms of female encephalisation quotients against those of conspecific males clearly shows that females of dimorphic species typically exhibit enhanced quotient values (see Figure 5.8). Moreover, no significant differences were found for any comparison between classes of males, including strongly dimorphic against monomorphic, whereas for females this comparison was highly significant ($p < 0.005$).

The results are most conveniently discussed with reference to Figure 5.11. This diagram highlights the divergence between dimorphic females (whether mildly or strongly dimorphic) as opposed to all the other categories, which together seem to comprise a separate, homogeneous group in respect of their Log EQ values. Although visual impressions can sometimes be misleading, especially if there is any distortion inherent in the scale adopted, in the present instance there seems no



MM MONOMORPHIC MALE
DM MILDLY DIMORPHIC MALE
SDM STRONGLY DIMORPHIC MALE
MF MONOMORPHIC FEMALE
DF MILDLY DIMORPHIC FEMALE
SDF STRONGLY DIMORPHIC FEMALE

Diagram illustrating average Log EQ values and standard errors (vertical line markers) for different catagories of simian primates. (After Willner & Martin, 1985)

reason to believe that the disposition of the groups is an artefact of the method of presentation selected. It should also be remarked that the differences cited in relative brain size have persisted despite the inevitable scaling down occasioned by the use of logarithmic transformations to achieve linearity in the brain:body weight relation. Yet notwithstanding, and although the sample sizes employed were restricted by the limited availability of brain weight data for adult animals of known sex, dimorphic females emerge as uniquely different from monomorphic females, as well as from all classes of males, with respect to their Log EQ values.

The considerable variability within groups is perhaps noteworthy in its own right. It has already been remarked that males of small-bodied dimorphic species tend to have rather higher Log EQ values than would be predicted according to the common trend, although to a lesser extent than females of the same species. It may be that, initially, both sexes of these species were selected for small body weight and that females then experienced further selection for an additional reduction in body weight relative to males of the same species. Yet it seems more parsimonious to suggest that environmental conditions favoured an overall reduction in adult body weight for both sexes, with a corresponding lowering in the age of attainment of sexual maturity. Intersexual differences in energetic needs and life history constraints presumably

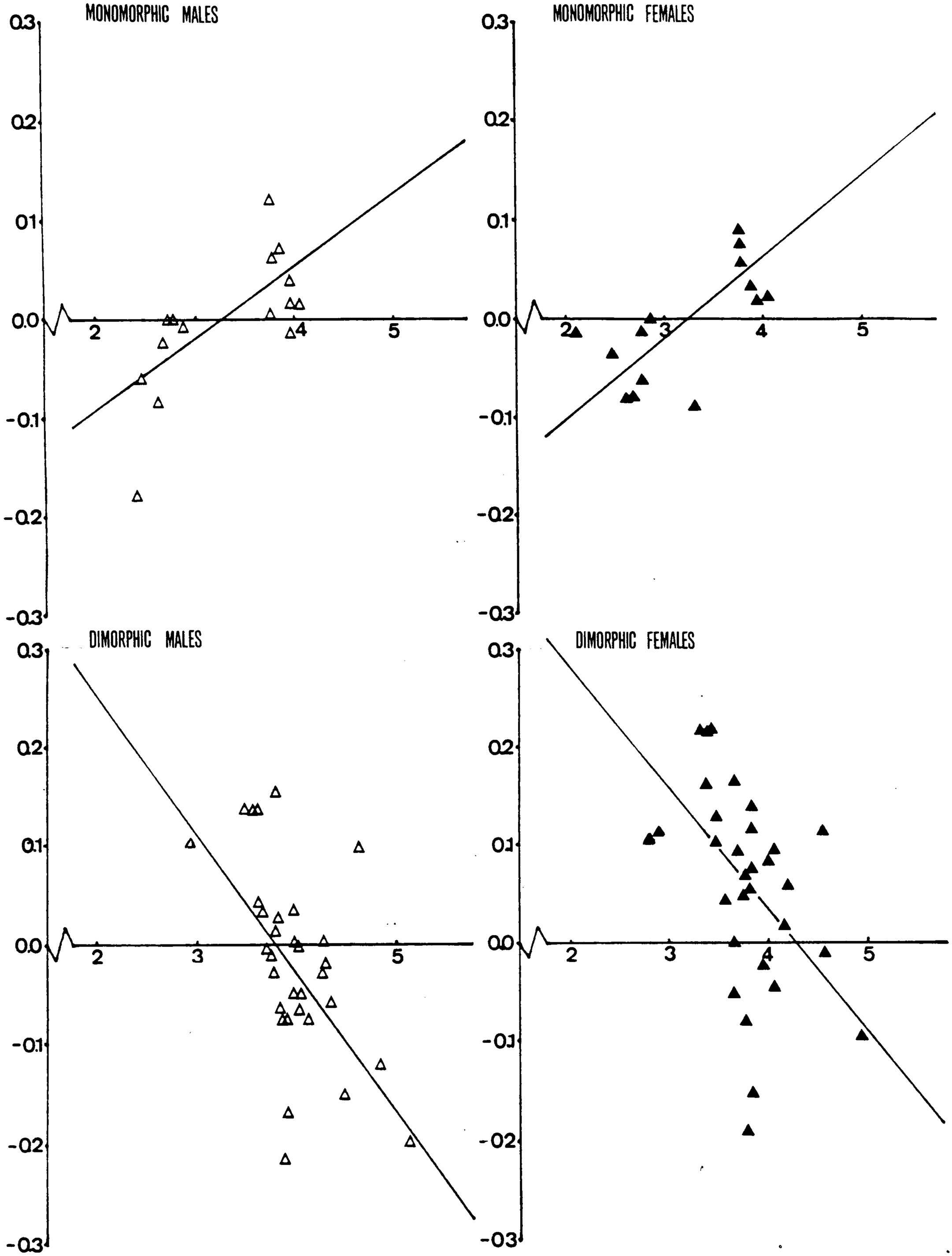
enabled this strategy to be more fully realised in females than in males. Among the larger-bodied dimorphic genera, differences in Log EQ values between males and females of the same species remain apparent, indicating that females persistently attain a smaller adult body size relative to that of the conspecific male. At the same time, selection for overall increase in adult body size has tended to mask this effect in comparison with other females. Thus, in its influence on intrasexual comparisons of Log EQ values, the effects of differential size selection operating on males and females seems to be reinforced by overall selection for small body size and countered by overall selection for large body size.

Even so, and despite the confounding effect of overall changes in species body weight, there is evidence that females of sexually dimorphic species have favoured a decrease in size to attain earlier first breeding than would otherwise have been possible. This raises an important issue, since on the basis of their mean Log EQ, males of these same dimorphic species show no sign of having been selected for an increase in body size. Yet some of these big males are extremely heavy and the group includes the largest known primates. Moreover, the social organisation of some species gives every reason to believe that they have been highly size selected (Dunbar, 1988). The apparent lack of evidence, in terms of Log EQ, for what appears to be an almost incontrovertible fact

initially seems somewhat remarkable. However, the explanation lies in the summary nature of the mean. In the preceeding examination of relative brain weights, inferences have rested on comparisons between mean Log EQ values estimated for groups of primates classified by sex and degree of dimorphism. Unfortunately, group means are rather insensitive parameters, since they give no indication of trends inherent within a group. To overcome this deficiency, the dispositions of the Log EQ values within the groups were examined. For monomorphic and dimorphic categories combined, no significant association was found between Log EQ and Log body weight for either males or females. However, when the same analyses were carried out separately within each of the four categories of dimorphic and monomorphic males and females, some striking relations emerged (see Figure 5.12).

It is of course quite unremarkable that if a correlation arises between Log EQ and Log body weight for any subset of the data, then the remaining data will generate an association of the opposite sign. This stems from the definition of Log EQ as the displacement of a recorded value of the logarithm of brain weight from the average, or expected value at a particular body size. What is not obvious, and consequently of interest, is why any relationship should emerge when the total data set is partitioned between monomorphic and dimorphic species. It has already been noted that no association was found

FIGURE 5.12



Logarithmic plot of encephalisation quotient against body weight for male and female simian primates

within the complete data set, taken as a whole; this would have been equally feasible for the subsets examined. It seems counter-intuitive to assume that the strong correlations that characterise these subgroups are merely spurious and have arisen in the absence of any underlying relationship.

Among dimorphic species, strong negative associations were found between Log EQ and Log body weight for both males and females ($r = -0.58$, $p < 0.001$ and $r = -0.46$, $p < 0.01$ respectively). Since the ancestral primate was almost certainly small (see page 194), these correlations suggest that both sexes of the larger species have been selected for increased overall body size. This was presumably tempered, in the case of females, by the attendant opportunity cost of delayed first reproduction that typically accompanies an increase in adult body size (Ralls, 1977; Downhower, 1976; Clutton-Brock et al., 1977). Among the smaller-bodied dimorphic species, selective pressure towards a reduction in body size has probably been more fully realised among females. It seems likely that all females of sexually dimorphic species have experienced a reduction in adult body weight, relative to some hypothetical species value, and that this is reflected in an inflated value of the mean Log EQ. In contrast, it is possible that males have been subject to intensive selection for increased body size among the larger-bodied dimorphic species alone; in consequence, the

group mean Log EQ for dimorphic males is not significantly less than that of either monomorphic males or monomorphic females. Nevertheless, the highly significant negative correlation between Log EQ and Log body weight within this group suggests that the larger-bodied primates have increased in overall size in relatively recent time.

A very different pattern emerged among monomorphic species, with a highly significant positive correlation arising between Log EQ and Log body weight for both sexes ($r = 0.74$; $p < 0.01$ and $r = 0.79$; $p < 0.001$ for males and females respectively). However, a plot of the data suggests that this finding does not reflect the usual type of association between two variables (see Figure 5.12). Instead of the usual scatter of points about a line, which may then be interpreted as expressing an underlying functional relationship, there are two discrete clusters of points. Indeed, viewed in this light, the high correlation appears to stem from the emergence of two contrasting groups within the general class of monomorphic simian primate. The smaller species together seem to comprise one category and the larger-bodied hylobatids and spider monkeys another. Moreover, results from a detailed examination of the allometric relation between brain weight and body weight within the general class of monomorphic simian primates lent further emphasis to this apparent dichotomy. The 95% confidence interval for the major axis gradient estimated for the complete

sample of monomorphic simian primates, spanning the entire weight range, was found to be 0.797 - 0.846. However, when calculated separately, the gradients of the major axes for large-bodied and small-bodied forms both lay outside these limits. The small-bodied species yielded a gradient of 0.868, which exceeded the upper limit, whereas the gradients obtained for the larger species (b=0.455 for lesser apes and spider monkeys taken together, b=0.523 for lesser apes alone) were well below the lower limit for the entire sample. These findings suggest that the two groups may constitute different grades.

It also transpires that, although both sexes share a common body weight, absolute brain size in males typically exceeds that of the conspecific females among most of the bigger species whereas no such divergence is apparent for any of the smaller species (see Figure 5.5). A possible explanation would be that the larger genera have reverted to monomorphism after a period of sexual size dimorphism. This would account for the curious distinction between large and small-bodied forms. On the assumption of a small, monomorphic ancestor, then the same conditions which favoured an overall increase in adult body size might well have carried with them opportunities for more flexible timing of first breeding (Downhower, 1976; Clutton-Brock et al., 1977; Ralls, 1977). A subsequent deterioration in the environment might then have been conducive to a deferment in the age of first reproduction

in females, leading to a resumption of monomorphism. In support of this interpretation it should be noted that, in contrast to all the other larger-bodied simian primates, the monomorphic species alone are monogamous, a system which tends to evolve under conditions calling for shared parental investment (Kleiman, 1977; Wittenberger and Tilson, 1980). If this change occurred relatively recently in evolutionary time, the female brain would still be targeted at the smaller size associated with her previous role as the smaller-bodied, earlier-breeding partner in a sexually dimorphic phase. The fossil record supports this hypothesis in respect of the lesser apes (Fleagle et al., 1980).

Fleagle and his colleagues found evidence of sexual size dimorphism in three species of primates from the Oligocene of Egypt. Since these are among the earliest known fossil anthropoids it seems likely that sexual size dimorphism represents the primitive condition for Old World higher primates, including gibbons and siamang. Moreover, the latter species are aberrant in another respect. R.I.M. Dunbar (pers. comm.) reports highly significant associations among primates between group size and percentage of time spent grooming as well as between each of these variables with neocortical weight relative to body weight. But the hylobatids do not conform to this general trend. They spend less time grooming and the family groups they favour are much smaller than expected

on the basis of their brain size. However, if their relative brain weight is 'inflated' on account of a reduction in overall body size following an earlier dimorphic phase, then this anomaly is neatly resolved. The balance of probabilities seems to favour this interpretation of the presently available data.

There remains the strange absence of correlation between adult brain and body size among females of at least two groups of sexually dimorphic species, in contrast to the significant associations found for males of these species. Although there was insufficient data to pursue this line of enquiry for additional groups of species, the evidence from cercopithecines and macaques suggests that sexual dimorphism has originated in these genera through a relatively recent change in female body size so that selection has not yet had time to re-establish the optimum relationship between brain and body weight. This interpretation is entirely consistent with previously noted anomalies in the Log EQ values of these females.

At the same time, it would be wrong to ignore the lack of association between body weight and brain weight found among species of baboon for either males, females, or males and females together. However, it is probably true that for these large monkeys both sexes have been heavily selected for increased body size, with females

favouring a lower adult body weight than males. If this adaptation has occurred during the relatively recent evolutionary past, then it would account for the low correlation noted for each category. Although such a post hoc explanation is not entirely satisfactory, it is at least plausible and in accordance with the available facts.

Thus, despite certain confounding factors, it has been possible to exploit the anomalies which result from the interaction of brain ontogeny with changes in body size. Analysis of relative brain sizes of simian primates, which constitute a well-defined evolutionary grade, shows that females of dimorphic species tend to have larger brains than expected, not only in comparison with males of the same species, but also in comparison with females of monomorphic species. Whilst males of strongly dimorphic species have smaller brains (relative to body size) than conspecific females, they do not differ significantly from males of monomorphic species in terms of mean Log EQ. Accordingly, the evidence from scaling of the brain in simian primates suggests that sexual size dimorphism has been promoted by body size reduction in females. The divergence appears to have been further accentuated by an increase in overall size among the larger-bodied males.

The approach adopted above was only possible because of the unusually early stage in ontogeny at which brain

growth is virtually completed. The fact that teeth also mature early in mammalian development affords an alternative means for probing the evolution of sexual size dimorphism. Relative tooth size can be used as a key parameter in an analysis which precisely parallels that already carried out for relative brain size. A degree of consistency in the two sets of findings would lend further credence to the belief that a reduction in adult female body size, associated with a lowering of the age of first reproduction, has been a major factor in the the evolution of sexual size dimorphism, at least for simian primates. Conversely, lack of consistency between the results based on these two early maturing components would inevitably undermine the strength of the hypothesis in accounting for the known facts.

The following section examines the dental evidence.

CHAPTER 6

THE DENTAL EVIDENCE

6.1 Overview

This chapter is somewhat in the nature of an appendix, or postscript, seeking to corroborate inferences based on the allometric scaling of the brain. As already intimated, teeth, like the brain, are early maturing entities. It follows that the allometric relations between tooth area and body weight for males and females of both monomorphic and dimorphic species should mirror those already noted for the brain. In order to test the hypothesis that females of sexually size dimorphic species have undergone a reduction in adult body size, a measure of tooth size (see below), relative to overall body size, was examined in terms of an index, Log ID. This was defined in the same way as those previously used to investigate brain size, age at sexual maturity, lifespan and maternal investment, namely Log EQ, Log IL, Log IM and Log IG. It was here predicted that the log ID values would discriminate between dimorphic females and all other categories, namely monomorphic females and both monomorphic and dimorphic males. In particular, to be consistent with the

previous results in respect of relative brain size, the Log ID values for dimorphic females should systematically exceed those of the conspecific males. In addition, the mean Log ID for dimorphic females had to be significantly greater than that for any other class of simian primate, with no significant differences arising between these. The analysis presented below shows that each of these predictions is individually fulfilled and that the overall findings are completely in harmony with the stated hypothesis.

The force of this concurrence would be further strengthened if it could be shown that tooth size scales in the same way as brain size. It is known that the slope of the major axis for a logarithmic plot of brain weight against body weight is much lower when it is estimated for a group of related species than when obtained for a wider range of species and that it takes an even lower value when calculated for an interspecific plot (see Martin and Harvey, 1985). It will here be shown that the allometric coefficients for tooth size follow a similar pattern, decreasing with the degree of relatedness of the species for which they are calculated.

However, each of these calculations requires a suitable frame of reference and, whereas brain weight is a conveniently unambiguous measure for an allometric study, there is no similarly unique basis for an

examination of dental allometry. Before this could be attempted, it was first necessary to decide which tooth (or teeth) would afford the most appropriate standard for comparison and which dimensions would yield the best estimate of size.

6.2 The data

6.2.1 Choice of reference tooth

Extensive research has shown that the central molars are the least variable teeth in the primate dentition (e.g., see Gingerich, 1974, Gingerich and Schoeninger, 1979). These are consequently the best teeth on which to base an allometric analysis. R.D. Martin (pers. comm.) has advocated the use of the total cheek tooth area, on the grounds that this represents the entire region that is primarily involved in the chewing and processing of food. However, the size of an individual tooth is, in itself, subject to a degree of variability and to use dimensions spanning several teeth would inevitably lead to an overall increase in the variance of the measurements obtained. The comparative nature of the present study made any increase in variability particularly undesirable, since real differences between groups might be obscured by a high level of within group variation. It was decided to focus on the dimensions of a single tooth in an attempt to minimise this risk. There then remained the task of determining which individual tooth would be the most suitable representative.

Gingerich (1974) found that upper and lower first molars were the least variable teeth for a range of mammals, a finding supported by a later study of additional species (Gingerich and Winkler, 1979). However, these results were contradicted by work on other species (Gingerich and Ryan, 1979), from which the second molar emerged as the least variable tooth. Discussing these inconsistencies, Gingerich and Schoeninger (1979) concluded that "the position of lowest size variability is centred over different cheek teeth according to the length and conformation of the cheek tooth field". In general, they advocated the use of either upper or lower first or second molars for comparative purposes. The lower first molar was selected as the focal tooth for the present study; any one of the suggested alternatives would, presumably, have been equally suitable, but one tooth had to be chosen from the range of possibilities. An appropriate measure of size was then needed.

6.2.2 Assessing tooth size

Following Gingerich et al., 1982, crown tooth area (mesial-distal crown length multiplied by buccal lingual width) was adopted as the measure of tooth size. As remarked by these authors, crown area is based on two independent, orthogonal measures of the same tooth, so that it is likely to give a more accurate estimate of size than could be achieved by a single measure. For the same

reason, differences in crown shape should have less influence on crown area than on either of the single dimensions of length or width. In fact, Gingerich and his colleagues found that, within a group of noncercopithecoid species in their study, although the frugivores had short, broad lower molars whilst the folivores species had long, narrow lower molars, the distinction between them lay only in the shapes of their teeth. There appeared to be little or no difference in relative crown area. These same frugivorous species had previously been reported as having small teeth for their body size, on the basis of a length measuremant alone (Kay, 1975).

6.3 The analysis

The current analysis was restricted to measurements taken from simian primates alone, since prosimians probably constitute a separate grade in terms of dental morphology as well as in other respects (see page 196-198). Their distinctive dietary habits (e.g., gum feeding) must surely have led to a degree of dental specialisation which would differentiate them from other primates.

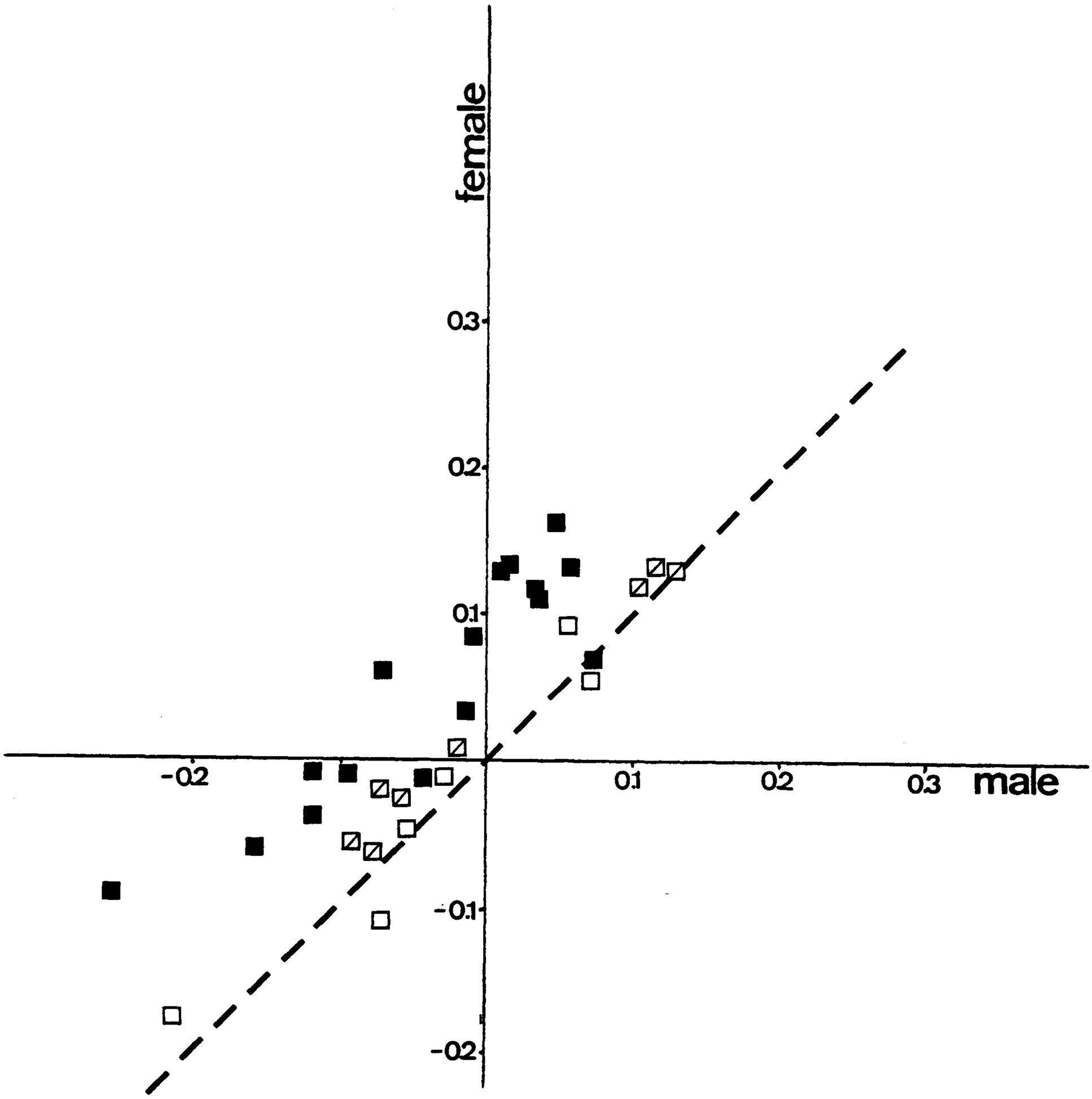
As in the previous analysis of Log EQ values, it was again essential to obtain unbiased estimates of Log ID values for comparisons between the sexes. This was achieved by calculating Log ID values for males and females of each species relative to the common major axis of a logarithmic plot of molar tooth area against body

size. The 95% confidence interval for the slope of the combined major axis (0.52 - 0.58) for male and female data taken together, included the slopes obtained for males and females taken separately (0.54 and 0.57 respectively), so that the procedure was justified.

6.4 Results

The results obtained precisely mirrored those reported in Chapter 5 for Log EQ values and thus corroborated the potential implications of Figure 5.6 regarding intersexual differences in relative brain size. Females of dimorphic species generally had greater Log ID values than males of the same species, whereas in monomorphic species this trend was barely apparent, with males of two species actually having slightly higher Log ID values than females (see Figure 6.1). Since females are characteristically smaller than males in primate species in which sexual size dimorphism is at all pronounced, it was to be expected that the direction of the enhanced index values, this time Log ID, would favour females.

The scope of the present research does not extend to analysing the respective male and female Log ID values for non-primate species with the female the larger sex. Nevertheless, it is anticipated that among such individuals the Log ID values would be smaller for males, as previously predicted for Log EQ values. In general, higher values for both Log ID and Log EQ would arise in



DOTTED LINE DENOTES EQUIVALENCE OF MALE AND FEMALE LOG ID VALUES

- □ MONOMORPHIC
- ▨ MILDLY DIMORPHIC
- ■ STRONGLY DIMORPHIC

Plot of log ID values for female simian primates against those for males of the same species.

connection with the smaller-bodied sex as compared with the opposite sex.

The results that emerged from the dental analysis replicated the pattern based on relative brain size in every respect. Differences between the indices calculated for males and females, now Log ID instead of Log EQ were again most pronounced in species showing marked sexual dimorphism (male:female body weight ratio greater than 1.3) as compared with species exhibiting only mild sexual dimorphism (see Tables 6.1, 6.2, 5.2 and 5.3). Student t-tests based on the group means yielded no significant difference between male and female Log ID values for monomorphic species, whilst the difference for dimorphic species attained a significance level of $p < 0.005$. Subdividing the dimorphic group into two sub-classes of strongly and mildly dimorphic species, the group means for males and females of the first category differed at a significance level of $p < 0.005$, whereas for the second category the difference in the intersexual group means failed to attain significance.

In view of the relatively small sample sizes (males from 8 species and females from the same 8 species) and the inherent variation within each of the groups, it is not surprising that the difference between the mean Log ID values for these less divergent categories was not statistically significant. This also occurred with the

TABLE 6.1

DIFFERENCES BETWEEN FEMALE AND MALE LOG ID VALUES CALCULATED FROM THE COMMON MAJOR AXIS

	LOG ID MALE (A)	LOG ID FEMALE (B)	(B)-(A)	D
MONOMORPHIC SPECIES: D < 1.15				
Aotus trivirgatus	0.068	0.053	-0.015	1.03
Ateles geoffroyi	-0.216	-0.172	0.044	0.98
Hylobates klossi	-0.075	-0.106	-0.031	1.04
Hylobates agilis	-0.053	-0.044	0.009	1.07
Hylobates moloch	-0.007	-0.022	-0.015	1.05
Saguinas geoffroyi	0.054	0.099	0.045	0.98
MILDLY DIMORPHIC SPECIES: D =< 1.3				
Alouatta seniculus	0.134	0.132	-0.002	1.26
Alouatta villosa	0.116	0.124	0.008	1.30
Colobus badius	-0.057	-0.027	0.030	1.15
Macaca mulatta	0.097	0.118	0.021	1.17
Pan troglodytes	0.000	0.012	0.012	1.23
Presbytis cristata	-0.084	-0.055	0.029	1.19
Saimiri oerstedii	-0.072	-0.062	0.010	1.20
Saimiri sciureus	-0.024	0.001	0.025	1.15
STRONGLY DIMORPHIC SPECIES: D > 1.3				
Cebus apella	0.033	0.102	0.069	1.49
Cercocebus albigena	-0.006	0.011	0.005	1.37
Cercocebus galeritus	0.048	0.153	0.105	1.86
Cercocebus torquatus	0.012	0.133	0.121	1.81
Cercopithecus aethiops	-0.032	-0.005	0.037	1.41
Cercopithecus ascanius	-0.119	-0.042	0.077	1.45
Cercopithecus cephus	-0.014	0.033	0.047	1.41
Cercopithecus mitis	-0.117	-0.002	0.115	1.72
Cercopithecus mona	-0.072	0.054	0.126	1.76
Cercopithecus neglectus	-0.091	-0.007	0.084	1.72
Cercopithecus nictitans	-0.159	-0.054	0.105	1.56
Colobus polykomos	-0.076	-0.018	0.058	1.44
Cynopithecus niger	0.065	0.061	-0.004	1.35
Gorilla gorilla	-0.009	0.087	0.096	1.69
Macaca fascicularis	0.051	0.129	0.078	1.52
Macaca nemestrina	0.008	0.131	0.123	1.79
Nasalis larvatus	-0.257	-0.097	0.160	2.15
Pongo pygmaea	0.025	0.112	0.087	1.98

MEANS & STANDARD ERRORS:	MALES (A)		FEMALES (B)	
MONOMORPHIC	-0.0382±0.0424	(6)	-0.0320±0.0407	(6)
MILDLY DIMORPHIC	0.0138±0.0314	(8)	0.0304±0.0290	(8)
STRONGLY DIMORPHIC	-0.0394±0.0200	(18)	0.0434±0.0175	(18)
ALL DIMORPHIC	-0.0231±0.0173	(26)	0.0394±0.0148	(26)

TABLE 6.2

INTERSEXUAL AND INTRASEXUAL DIFFERENCES IN MEAN LOG ID VALUES ACCORDING TO DEGREE OF SEXUAL SIZE DIMORPHISM

1) INTERSEXUAL DIFFERENCES : PAIRED t-TESTS

	MEAN DIFFERENCE	t	n	p
MONOMORPHIC: D < 1.15	0.0062	0.45	(6)	n.s.
MILDLY DIMORPHIC: D =< 1.3	0.0166	4.15	(8)	<0.005
STRONGLY DIMORPHIC: D > 1.3	0.0827	8.19	(18)	<0.0005

2) INTRASEXUAL DIFFERENCES (FEMALES)

(COMPARISONS BETWEEN GROUP MEAN LOG ID VALUES)

	t	n	p
MONOMORPHIC vs. MILDLY DIMORPHIC	1.29	(14)	n.s.
MONOMORPHIC vs. STRONGLY DIMORPHIC	2.11	(24)	<0.025
MONOMORPHIC vs. ALL DIMORPHIC	1.97	(32)	<0.05

3) INTRASEXUAL DIFFERENCES (MALES)

(COMPARISONS BETWEEN GROUP MEAN LOG ID VALUES)

No significant differences were found between any classes of males.

difference between the mean Log EQ values for these same classes. In order to offset the variation within groups, and following the same practice adopted in respect of Log EQ values, paired t-tests were carried out on the differences between female and male Log ID values within species. Once again, no significant differences were found between males and females of monomorphic species, but now the differences in Log ID values between males and females of only mildly dimorphic species were highly significant ($p < 0.005$) and those of strongly dimorphic species were significant to an even greater extent ($p < 0.0005$). The intersexual difference for all dimorphic species taken together also attained a significance level of $p < 0.0005$.

As already remarked in relation to Log EQ values, such findings only reveal the existence of persistent Log ID differences between males and females of sexually dimorphic species, without giving any indication of the direction of body size change involved. However, in harmony with the earlier finding in respect of Log EQ values, it appears that females of sexually dimorphic simian primate species generally have higher Log ID values than females of monomorphic species. This reinforces the argument previously advanced and suggests that a plausible explanation for both the higher Log ID and higher Log EQ values lies in a general trend to reduction in female body size in dimorphic species, with accompanying increases in the respective indices. The index values would be modified

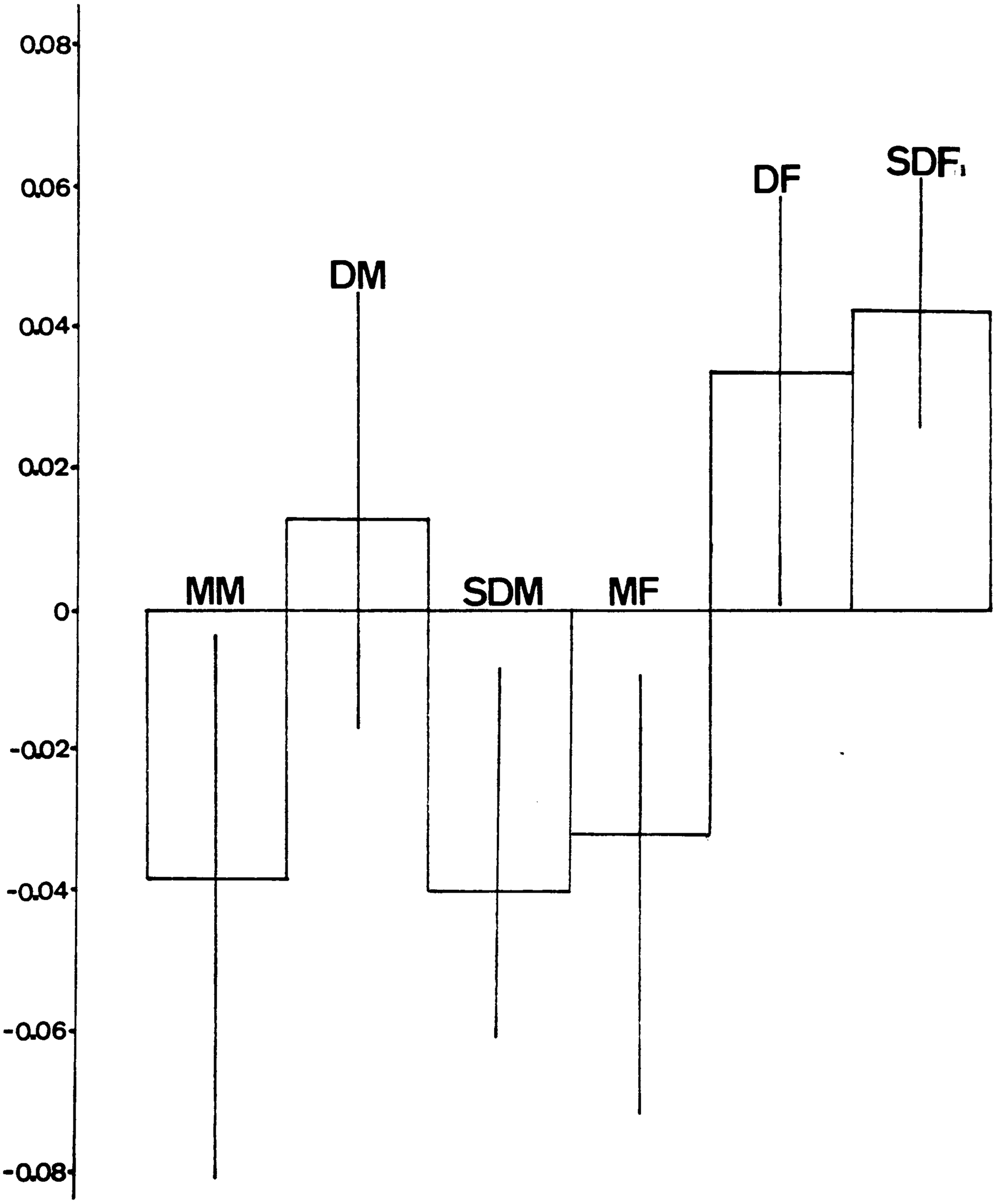
on account of the continued growth in overall body size that follows the ontogenetic stage at which brain development and tooth growth are complete. In respect of relative brain size, the degree of enhancement of the index was found to be tempered, though not entirely annulled, by selection for overall size increase in both sexes of the larger-bodied species, but to a lesser extent among males than females. This effect was entirely absent from the dental index, with no association emerging between Log ID and Log body weight for either males or females of dimorphic species. In contrast, and in conformity with the relation between Log EQ and Log body weight, significant negative correlations were found between Log ID and Log body weight for both sexes of monomorphic species ($r = -.0.77$, $p < 0.05$ and $r = -0.89$, $p < 0.01$, for males and females respectively).

A plot of the Log ID values of females against those of conspecific males clearly shows the tendency for females of dimorphic species to exhibit enhanced quotient values in respect of molar tooth area (see Figure 6.1), in addition to those already reported for brain size (see Figure 5.8). Once again, no significant differences were found for any comparison between classes of males, including strongly dimorphic against monomorphic, whereas the difference between these groups attained a significance level of $p < 0.025$ for females.

These findings can best be appreciated by reference to Figure 6.2. The divergence between females of sexually size dimorphic species, (whether mildly or strongly dimorphic) and all the other categories is as pronounced in respect of Log ID as for Log EQ (see Figure 5.11). Moreover, these differences have remained conspicuous in spite of the 'scaling down' which always accompanies the use of logarithmic transformations.

So far, the findings derived from the dental evidence have entirely vindicated the inferences made on the basis of the scaling of the brain. Nevertheless, the force of this complete coincidence would be strengthened if it could be shown that molar teeth scale in the same way as brain size, not only between species, but also within related groups of species and even within single species. It is well known that the allometric coefficient for brain weight against body weight is much higher when estimated from an interspecific plot for a wide range of species than when it is calculated for a group of related species (e.g., see Martin and Harvey, 1985). To further test the correspondence between the scaling of tooth crown area and brain weight, subsets of the dental data were examined for groups of related species.

For a range of simian primates of both sexes, tooth area scaled with an allometric coefficient of 0.58. However, the major axes for logarithmic plots of molar



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SDF STRONGLY DIMORPHIC FEMALE

Diagram to show average log ID values and standard errors (vertical line markers) of simian primates.

tooth size against body weight had much lower gradients when estimated for data from related species. There was insufficient data to permit such calculations to be carried out for more than three groups, and even then, the result obtained using the means for 3 species of mangabeys (3 values for males and 3 for females), were discounted since the level of association failed to reach significance. However, data from 7 species of cercopithecine ($n = 14$) and 3 species of macaque ($n = 6$) yielded significant correlations ($r = 0.67$, $p < 0.005$ and $r = 0.82$, $p < 0.025$ respectively. The gradient of the major axis for each of these groups, 0.25 for the cercopithecines and 0.32 for the macaques, was well below 0.52, the lower limit of the 95% confidence interval calculated for the full range of species.

It remained to examine the scaling of molar tooth area with body weight within a single species. In order to do so, measurements were taken from skeletal material kindly made available by the British Museum of Natural History. Fortunately, this included several specimens of Presbytis obscura and Cercopithecus mitis derived from animals of known body weight. Since all the previous analysis had been carried out with reference to body weights, it was a considerable advantage, in terms of comparability, to have such weight data. The molar tooth dimensions taken from these particular specimens are recorded, together with their individual weights, in

Appendix 2.5. The results of the analyses were inconclusive in respect of both species. The gradients calculated for the two major axes were 0.11 for the cercopithecine data (n = 12) and 0.67 for 19 individuals of Presbytis obscura. Whilst the former gradient was of the expected order of magnitude, the latter was higher than anticipated. However, neither correlation coefficient was significant. It may be that there is a genuine lack of association between tooth area and body weight within species; alternatively, there could be an underlying relation between these two entities which is masked by the variability inherent in the data. This second possibility should not be discounted. After all, the analyses between species were based on mean tooth dimensions and mean body weights, so that the variation between individuals was effectively eliminated. At an intraspesific level, this could have become a dominant factor. Nevertheless, in respect of the major axes gradients, the upper limit of the 95% confidence interval for Cercopithecus mitis, -0.11 - 0.34, was well below the lower bound of 0.52 calculated for the complete data set for simian primates. The 95% interval obtained for Presbytis obscura was so wide ranging (0.18 - 1.58) that no real meaning could be attached to it.

Taken overall, although no firm evidence could be adduced for comparability between the scaling of dental dimensions and that of brain weight within species, close

parallels emerged in other respects - that is, both between groups of related species and across a wider range of simian primates. Moreover, there were quite striking similarities between the configurations of Log ID and Log EQ values for the various categories of primate. The consistency of the results obtained from the independent, but complementary, analyses of molar tooth area and brain weight lends credence to the main thesis - namely, that a reduction in adult female body size, accompanied by the earlier attainment of sexual maturity, has played a major role in the evolution of sexual size dimorphism, at least in simian primates.

CHAPTER 7

CONCLUSIONS

7.1 OVERVIEW

Scaling is intrinsic to every biological function and many evolutionary problems can be restated in the single phrase: "how big is it and how fast does it happen" (Horn, 1978). In 1965 Taylor first commented on the regularity with which most mammals take the same proportion of their lives to reach the same proportion of their adult body weight (Taylor, 1965, 1968). More recently, Peters (1983) has remarked upon the consistency with which each developmental phase accounts for a constant proportion of a mammal's life, noting that "about 2% of the maximum life span is passed between conception and birth, about 3% is over at weaning, and the average mammal still has 90% of its maximum life span ahead when sexual maturity is achieved". Peters also asserts that the average age at death is roughly half the maximum span, but this seems to be an unsatisfactory tenet. The average age at death is liable to quite extreme variation between populations, on account of differences in habitat quality between different geographic areas, as well as those obtaining at different times within the same location. This would tend to undermine the strength of the relation between average

and maximum lifespan unless both of these had been recorded in the identical environment. Maximum lifespan data are typically derived from captive animals and may well converge asymptotically to the genetically feasible upper limit for a species. This single figure, supposedly representative of the species as a whole, and independent of local influences, is probably the most suitable for use in a comparative study and has been adopted here. It must nevertheless be accepted with some caution. Recent years have seen a trend towards increasing values for the maximum reported lifespan in a variety of species. Some of these may be due to better veterinary care and improved zoological practice and more closely approach the true maximum. Other 'new' data may reflect nothing more than the continued survival of species that have only recently been bred in captivity. Such data inevitably yield estimates of maximum lifespan far short of the true potential for either captive bred or wild individuals.

The timing of each of the major ontogenetic events, namely birth, weaning, sexual maturity and death, scales regularly with adult body size. Owing to the constraint this effectively imposes, selection for change in any life history parameter, such as age at first reproduction, will be associated with a corresponding change in overall adult body size. It is here proposed that selection

pressures have favoured intersexual differences in the age of first breeding and that sexual size dimorphism has arisen as an inevitable corollary.

It is quite easy to envisage an evolutionary sequence leading from a small, monomorphic ancestral mammal, with both sexes attaining sexual maturity at the same age and adult body weight, to larger, sexually dimorphic species with females typically attaining sexual maturity at an earlier age than the conspecific males. As discussed in section 3.3 (page 77 et seq.), an overall increase in body weight would have opened up new possibilities and permitted differences in the optimum breeding strategies of males and females to be more fully realised, with a concomitant divergence in their respective adult body weights.

Cutler (1979) commented that ".....many variables determine the effects of environmental hazards on a species. One important parameter is the ability of the organism to learn from its environment in order to better adapt, protect and feed itself. A good correlation exists between the ratio of learned vs. instinctive behaviour and maximum lifespan". This relation should be as valid for age at first breeding as for maximum lifespan, since a change in the age of first breeding inevitably alters the

ratio of learned to instinctive behaviour at this critical and potentially dangerous stage in an animal's life history. It follows that the importance of learned behaviour in a particular environment will have a powerful influence on the extent to which an individual might benefit from a change in the age at first reproduction. The immediate effects of any such adjustment would differ greatly between males and females.

Male reproductive activity is beset by the dangers of overt intrasexual competition for matings with oestrus females. Lack of experience could well prove fatal to a young male that challenges an older animal for access to this vital resource. Indeed, the generally styled 'multi-male' type of organisation is now frequently seen to be 'age-graded', in harmony with Crook's (1972) assessment that "young sexually mature males are unlikely to be large enough, experienced enough or socially skilled enough to compete effectively with older animals, particularly in the context of sexual and sex-bonding behaviour". He further noted that attempts at too early an age could be "not only futile but damaging both physically and psychologically." It is quite feasible that these young males, although sexually mature, avoid potentially dangerous conflicts by abstaining from reproductive activity. Jones and Harvey (1987) remarked that many

animal displays serve to ensure that individuals fight only with rivals of the same rank and avoid costly attacks on competitors that would be almost certain to defeat them. The silver-back condition among gorillas and the throat flanges of orang-utans, as well as the heavy manes of several species of baboon also advertise the fully grown status of mature adult males.

Delayed first breeding also occurs in another context. Both male and female sibling helpers postpone their own reproduction despite being sexually mature. However, in some environments this would seem to be wasteful unless accompanied by an increase in overall body size; better, surely, to continue growing if this is a feasible option. Given the possibility, it is easy to see that selection might favour larger males. The biggest individuals would then automatically be those that had most successfully exploited the available nutritional resources. These same animals would subsequently benefit from a competitive 'edge' in respect of intrasexual selection, thus promoting a general increase in male body size for the species. This interpretation goes a long way towards explaining the strange dislocation between initial fertility and full development in male gorillas and orang-utans, each of which occurs in conjunction with extreme sexual size dimorphism.

Clutton-Brock (1974) emphasised that "when a novel adaptation evolves, its form will be partly determined by the various environmental factors through which selection is operating and partly by the species' phylogenetic inheritance". He concluded that this would lead to the evolution of "different traits with similar functions". This is nowhere likely to be more true than in respect of male and female reproductive strategies. Both sexes will be selected to maximise their breeding potential, but they may well have travelled very different adaptive routes to reach this common goal. Crook (1972) considered that a relaxation in food poverty would obviate the necessity for 'surplus' males to range separately from the reproductive unit. Provided the habitat could sustain all group members at an adequate nutritional plane, then male dispersal would cease to be of any particular survival value to either sex and might be more than offset by benefits related to enhanced social cohesion and reduced predation. The ensuing multi-male organisation is characteristically associated with varying degrees of intersexual differences in adult body size across a wide variety of taxa, including macaques, langurs, vervets and chimpanzees.

There is also evidence from several sexually dimorphic species that the sex ratio at birth responds to

changes in resource availability. Verme (1969) found that female white-tailed deer maintained on a low nutritional plane produced 70% sons, compared with 47% for females reared on a high plan of nutrition. Clutton-Brock (1982) similarly reported that a number of ungulate species produce more males at high population density. Among baboons and macaques, socially dominant females (presumably with better access to the available food supplies than their subordinates) produce more daughters than sons. This feature has also been ascribed to the linkage of a female's reproductive success with the rank of the matriline from which she stems (Altmann, 1980; Clutton-Brock, 1982). The two aspects are probably mutually reinforcing and it is conceivable that selection favours the earlier attainment of female sexual maturity as well as a preponderance of female births among well nourished populations. Since females are the limiting resource, this could enhance the reproductive output and evolutionary potential of the species as a whole. Colonisation of an enriched habitat with easier access to an adequate diet might favour increased body size among adult males while simultaneously enabling females of these same species to initiate breeding at an earlier age and smaller adult body size.

Frisch (1975) found that the fertility rate of a

non-contracepting human population could be linked to nutritional standards. She also reported a significant correlation between survival and birth weight for human neonates. Eastman and Jackson (1968) previously established an association between birth weight and both the prepregnancy weight of the mother and her weight gain during pregnancy, each acting independently and with additive effects. There is further evidence from human populations that inadequate nutrition results in "delayed menarche, longer than usual adolescent sterility, irregularity or cessation of menstrual function, higher pregnancy wastage, longer lactational amenorrhea" (Frisch, 1975). These findings presumably apply equally to non-human primates and, taken together, suggest that reproductive success in general and infant survival in particular depend on females attaining an appropriate physiological condition. The hypothesis that first breeding at an earlier age is only feasible in a relatively benign environment is further corroborated by the more frequent occurrence of reproductive errors at the beginning and end of the fertility curve (Frisch, 1977).

At the same time, even assuming unrealistically plentiful supplies of all resources, there must surely be a developmental constraint on the extent to which the age at first reproduction can be advanced. Among women,

normal growth of the uterus is completed late, at about twenty two years of age and the bony pelvis still later, at about twenty five to thirty years (Frisch, 1977). On the basis of her studies of such diverse taxa as humans and cattle, the same writer concluded that, if a female is bred too young, it might be at the expense of the completion of normal growth and could result in both an inferior offspring and the death of the mother. It is unlikely that nonhuman primates differ in either of these respects or in relation to the interbirth interval, which is typically longer for poorly nourished women (Frisch and McArthur, 1979). The benefits of initiating reproduction at an earlier age and smaller size might be more than offset by an extended interbirth period, especially since smaller individuals are typically at a disadvantage in competing for scarce resources. This could be a major factor among certain species, such as vervets, for which failure to attain breeding condition at the appropriate season results in reproduction being delayed for a full twelve months (see p.80).

From an evolutionary perspective, the net effect of the increased risks to the primiparous mother, possibly in conjunction with an extended interbirth interval, would be to temper the enhanced fitness that might otherwise ensue from earlier first breeding. However, the balance between

the opposing selection pressures is likely to vary according to overall maternal body weight. Thus, whereas gorilla and chimpanzee neonates are about the same weight at birth, the smaller size of the gorilla neonate relative to the mother's weight may permit the female gorilla to breed successfully before uterine and pelvic growth is complete. There is quite simply an increased margin of safety between the size of the neonate and the mother's pelvic dimensions. In general, bigger females can probably initiate earlier breeding at a relatively smaller body size with much less risk than would be incurred by an absolutely smaller individual. Males of these same species are likely to have been heavily size selected. Sexual size dimorphism is consequently more likely to be strongly developed among large bodied species.

Thus far, the sequence of events described is merely plausible. The present research makes its contribution by adding the weight of quantitative evidence to these preliminary speculations, enabling them to be restated as formal hypotheses based on verifiable facts. This is intrinsic to the approach that has been adopted throughout the study. At each successive stage an attempt has been made to seek out quantifiable attributes capable of discriminating between alternative evolutionary theories. When practicable, the subsequent comparisons have been

based on directly measurable variables, as in the allometric analyses of brain weight and molar tooth area. In other instances it has been necessary to resort to composite variables, such as the fetal growth factor. At all times, due consideration has been given to the possibility that grade effects might bias the findings. The data were always scrutinised with two complementary aims - to discover the existence of common, unifying factors and to expose any anomalies that might serve as indicators of evolutionary trends. Since inferences were prompted by the nature of correlational data, it was important to ensure that these were free from the confounding effects of contaminated variables. The work presented here claims the distinction of explicitly recognising this problem and at least attempting to subject it to a proper quantitative appraisal.

7.1.1 Confounded significance levels

Cogent reasons have been advanced for exercising restraint in the attribution of formal statistical significance to results based on correlational data (see 2.3). This appears to be a timely caution in view of a paper published in 'Nature' as recently as 1985. Harvey and Zammuto here affirm that they have demonstrated "...that the age at which females first reproduce is strongly correlated with expectation of life at birth,

after the effects of body size have been removed...". But what of the confounding effect of time to first reproduction being included in total lifespan? It would surely have been more appropriate to examine the relation between age at first reproduction (AR) and mean life expectancy (MLE) after the attainment of this age, rather than to focus on the correlation between AR and AR+MLE. This criticism should not be taken to imply that the association adduced is spurious, but rather that it should not be accorded a formal significance that might be misleading. Controlling for the effects of body weight is insufficient to ensure that the results will not still be distorted if one of the key variables is contained within the other.

7.1.2 A model for sexual size dimorphism

Cheverud and his associates (1985) conceived a model in which the value of a particular trait (T) in a species was broken down into a phylogenetic, or inherited value (P) and a specific value (S) due to independent evolution:

$$T = P + S$$

This particular representation has here been criticised for neglecting the sexual component (see pages 60-63). The use of mathematical modelling techniques to describe multivariate systems is not new. However, their utility, and even more importantly, their validity, depends on the

inclusion of all the relevant variables and due recognition of their possible interdependence. Although there are many species- specific adaptations that may be common to both sexes (e.g., digestive specialisations among folivores), adult body size is certainly not one of these and a model which purports to represent it, whilst ignoring its sexually mediated aspect, is fundamentally unsound. However, the introduction of an additional, sex-related variable (X) into the equation immediately redresses the situation:

$$T = P + S + X$$

The model is now hypothetically capable of responding to the sex-linked factors whose effects find expression in a sexually dimorphic trait. Throughout the present study, the trait under consideration has been adult body weight. The conceptual framework described leads this to be conceived of as the resultant of phylogeny, speciation and sex. Although no further mathematical analysis has been undertaken, this format is relevant to the general approach adopted since it leads directly to the rejection of average species values for traits that differ between males and females. This is partly because the mean value may never be attained by individuals of either sex, but more particularly because the existence of a <u>species</u> value will be illusory in respect of any trait that is of differential benefit to males and females. It is pertinent

here that, throughout their growth, the body weights of castrated java macaques are intermediate between those of intact males and females and closely approximate to the average for the species (Spiegel, 1956).

It is believed that differences in X, the sex-linked factor in the regulation of adult body size, result from divergent male and female life history strategies. All the findings of the present study reinforce this assessment. The contrasting experiences of the two sexes within their common environment were first referred to in Chapter 3, as a precursor to the subsequent more quantitative analysis. A further appraisal of these is now deferred to the concluding section of this chapter, in which an attempt will be made to integrate the new findings of this research with existing theory.

7.2 RELATIONS BETWEEN LIFE HISTORY PARAMETERS

In view of the previous remarks it is ironic that data on maximum lifespan were not separately available for males and females. Nevertheless, despite this limitation, significant associations were found between lifespan and age at sexual maturity (but see discussion below) as well as between lifespan and brain weight for both male and female mammals. Major grade distinctions were apparent but, since these appeared to make no appreciable

difference to the slopes of the best-fit lines, they should not have detracted from the overall validity of the results.

The key finding was probably the highly significant correlation that emerged between the logarithms of age at sexual maturity and brain weight. The importance of this result lies in the robust nature of the association, which persisted even when body weight and lifespan were controlled. The relation is even more striking when contrasted with the fragile association between lifespan and brain weight, which lost significance when controlled for age at sexual maturity, either alone or in association with body weight. This clearly undermines the biological relevance of the initial association. Although Sacher (1959) remarked that lifespan was more highly correlated with brain weight than with body weight, this could merely reflect brain size being less variable between individuals than body size, a view endorsed by the weight of the adrenal gland being an even better predictor of lifespan than brain weight (Economos, 1980b). It seems that the linkage between lifespan and brain weight may be no more than a secondary consequence of the association between lifespan and age at sexual maturity, a view that gains further support from an unresolved anomaly arising within Sacher's interpretation of his results. Economos (1980a)

has pointed out that the "hypothesis that a larger index of cephalisation (intelligence) effects a longer lifespan does not account for interorder differences in lifespan". Thus, in comparison with carnivores, higher primates have higher indices and longer lifespans, but rodents have smaller indices and similar lifespans while ungulates have similar indices in conjunction with shorter lifespans. Inferences based on correlational data are inevitably prone to reversals if an intervening variable has been omitted from the original set. The evolutionary interpretation favoured here is that a fundamental relation exists between brain size and age at sexual maturity, with lifespan linked to age at sexual maturity (see also Harvey et al., 1987).

However, these comments are very much in the nature of preliminary observations. In the first place, the analyses described are confounded by the inclusion of the time taken to reach the age of sexual maturity in the value used for total lifespan. In addition, female reproductive lifespan is likely to have a much greater influence than maximum lifespan on the evolutionary success of a species. This surely hinges less on longevity than on how age at first breeding affects the duration of a female's reproductive life. If early maturation leads to cessation of reproductive activity at a correspondingly

earlier age, then the potential benefits of such a strategy would be annulled.

It has already been remarked that different populations of the same species initiate breeding at different ages according to the quality of their habitat (e.g., vervets and elephants). These same populations should yield further insights as more data on either lifespan or life expectation become available. Lockyer (1978) also reported a striking reduction in the age at sexual maturity for both fin and sei whales following an increase in food supply. Intensive whaling in the immediate pre- and post-1930 years led to a gross depletion in the stocks of blue and fin whales. This presumably reduced the intensity of both intra- and interspecific competition for the available resources. Lockyer determined that the mean age at sexual maturity for fin whales fell from 10 years (pre-1930) to 6 years by 1955, with a similar result among sei whales - their mean age fell from 11.5 years pre-1935 to 7 years by 1960.

However, whatever impact the timing of first breeding makes on the subsequent reproductive life of either sex, this major landmark in an individual's life history is not reached until after the average mammal has already passed some 10% of its total lifespan (Peters, 1983). It is

therefore important to focus on intersexual differences in the developmental paths that lead males and females of sexually dimorphic species to become sexually mature at different ages and at different adult body sizes. A study of sexual size dimorphism that neglected this aspect would be damagingly incomplete.

7.3 ENDS AND MEANS: PATTERNS OF SEX DIFFERENTIATED GROWTH

Many attempts have been made to correlate sexual size dimorphism with such factors as body size, habitat type and mating system (e.g., Clutton-Brock and Harvey, 1977; Clutton-Brock *et al.*, 1977; Leutenegger, 1978; Leutenegger and Kelly, 1977; Leutenegger and Cheverud, 1982; Harvey *et al.*, 1978). These have enjoyed varying degrees of success, but they share a common failing. They ignore the dynamic processes of growth and concentrate on the static adult state. More recently, both Lee and Bateson (1984) and Shea (1986) have drawn attention to ontogeny as a potential source of new insights which would be denied to a study focused exclusively on adult endpoints. In their examination of the fuctional aspects of development, Lee and Bateson (1986) regard immaturity as an adaptive phase in the life history of an organism and emphasize that young animals are not merely imperfect adults with incomplete behavioural repertoires, but individual units behaving in ways that are relevant to their immediate

competence and survival. Shea (1986) has similarly stressed that natural selection is targeted on the entire pattern of sex-differentiated growth and not only the adult endpoints while Lande (1985) has argued that "individual differences in development produce phenotypic variation within populations". It is pertinent to question not only why adult males and females of the same species differ in size and shape, but also why they grow differently in the first place (Fedigan, 1982). This author also regards growth as more than simply a means to an end, and concurs with Shea in the belief that "perhaps it is the sex-differentiated growth pattern, as well as the final adult size, which is adaptive".

The present study indicated little or no selection for differences in male and female body weights at birth. This was attributed in part to the high correlation between birth weight and survival, which would militate against a reduction in the female birth weight. At the same time, the higher risk apparently incurred by the larger, faster growing males of some species (e.g., patas monkeys and elephants) would tend to counteract any benefits which might accrue from a general increase in male birth weight. The postnatal ontogeny of intersexual size differences was then examined. These were typically absent during infancy and the early juvenile period, but already pronounced by

first breeding. Following its inception, sexual size dimorphism became intensified through a combination of increased growth rate and extended duration of growth in the larger-bodied sex.

The present study consistently found a degree of bimaturism among sexually dimorphic species, with the large primate males becoming sexually mature later than the smaller females and male cetaceans initiating reproduction earlier than the larger females. Jarman's (1983) review of sexual dimorphism in large, terrestrial herbivores invokes sexual selection to account for the delayed first breeding of these large males, relative to the smaller females. He suggests that females will select mates on the basis of signals for survival, such as enhanced body size or 'weapons', so that "Males that eventually breed will be those that, as young males, adopted strategies of survival rather than competing dangerously for matings against the older males. Bimaturism will arise". This may well be true, but it is probably only part of the story. It certainly fails to explain the later breeding of female cetaceans, which do not compete between themselves for mates. However, it has been established for at least one of these marine mammals that depth of dive is strongly correlated with body size (Lockyer, 1977b). This might be of particular benefit to

females in their search for food. Males can range much more widely than is feasible for mothers in company with young. However, while it might be plausible to explain the delayed maturity in female cetaceans in terms of the extra time needed for them to grow to a bigger adult size, there is no certainty that this is a correct interpretation.

Whichever sex is the larger, the available data yield no clues as to whether delayed maturation is the response to selection for increased body size or whether selection for later first reproduction has facilitated continued growth to a larger adult body size. The same considerations, in reverse, would apply equally to earlier first breeding in conjunction with a reduction in adult body size. Analyses of correlational data are incapable of distinguishing between these two alternatives or indicating whether they are mutually reinforcing. They equally fail to reveal whether sexual size dimorphism is the product of an increase in the overall body size of the larger sex, or a decrease in adult body size of the smaller sex, or a combination of both of these. However, this latter problem has proved less intractable and has been resolved through an examination of intergroup trends in the allometry of the brain and molar teeth.

Shea (1986) commented on the degree of consistency

with which female cercopithecines of seven sympatric species reach sexual maturity and attain their full adult body weight at around four years, whereas males of the same species do not become sexually or physically mature until they are about six years old. Yet these same species show considerable variation in the extent to which they are sexually size dimorphic as adults. Since there is no evidence of prolonged male growth in any of these species (from the talapoin, with a male:female ratio of 1.23 to the mangabey, Cercocebus galeritus, with a ratio of 1.85), the entire range of sexual size dimorphism must be attributable to differences in the degree of differentiation between male and female growth rates. This is in marked contrast to the increased bimaturism that accompanies the pronounced dimorphism of the closely related patas monkey. The unusually precocious maturation of these females (at 2.5 years), earlier than any other cercopithecine, occurs in half the time it takes the male to mature, whereas in each of the other cercopithecine species females become both sexually and physically mature in two-thirds of the time required by males. This example serves as a useful reminder that bimaturism can occur as readily through precocious sexual and physical maturation in the female as through prolonged growth and delayed maturation in the male (see also Shea, 1986).

Shea (1986) cited further examples from other groups of related genera (e.g., macaques and baboons; chimpanzees and gorillas) to illustrate his central theme, namely, that "a given degree of sexual dimorphism may be produced in quite different ways, and correspondingly, various developmental trajectories may underlie an observed degree of dimorphism between two or more species". This fits neatly with the previously discussed concept of an organism constrained to achieve a state of equilibrium within its environment at each developmental stage. Data from the present study indicate that crab-eating macaques follow similar growth trajectories to those described by Shea for rhesus, pigtailed and bonnet macaques.

It is not yet clear how these findings should be interpreted in an ecological context. However, it seems that sexual dimorphism in some species is primarily a consequence of intersexual differences in growth rate, whilst in others it stems from differences between males and females in the duration of time taken to reach reproductive status and mature adult body size. These alternative developmental strategies may reflect different selection pressures, even when they lead to morphologically indistinguishable results (Gould, 1977; Shea, 1985, 1986). It is also likely that they represent different solutions to the fundamental problem of

maximising fitness by appropriately partitioning the available resources between the conflicting claims of continued growth and reproduction. The issues involved may be better understood in the context of energetic needs and maternal investment.

7.4 MATERNAL INVESTMENT AND REDUCED FEMALE BODY SIZE

Martin and MacLarnon (1985) showed that, per unit time and relative to maternal body weight, mothers of altricial neonates invest significantly more in their young prenatally than do mothers of precocial offspring. The current study contributes new evidence which complements this finding by showing that the same comparison exists between females of dimorphic and monomorphic simian primate species. The present analysis was restricted to data from monkeys and apes to avoid the possible confounding effects of grade distinctions, but it is anticipated that the result would be generally true for all mammals. Further research is needed to determine whether this expectation is fulfilled.

The discovery that females of dimorphic species invest relatively more in their offspring than mothers of monomorphic species might well have been anticipated. Since neonatal survival is highly correlated with birth weight, it is unlikely that earlier breeding at a smaller

maternal body weight would be a successful strategy if it involved a reduction in neonatal size. The smaller, younger mother must therefore invest more, relative to her own body weight, to ensure the viability of her offspring. So how can these inexperienced females afford such a high commitment? There appears to be no later postnatal compensation for this heightened early investment. On the contrary, Harvey et al. (1987) report that "primates that have slow prenatal development or give birth to relatively large young are also those that wean and mature relatively late in life". Birds follow a similar pattern (Lack, 1968).

It seems generally feasible that a relaxation in food poverty might have permitted females to breed successfully at an earlier age and smaller overall body size while simultaneously supporting an increase in male body weight. Indeed, it is difficult to envisage an alternative source for the 'extra' energy needed by these young, primiparous mothers during pregnancy and lactation. However, sexual size dimorphism is most prevalent among polygynous species, which are typically characterised by a high female population density. In fact, Emlen and Oring (1977) have argued that it is precisely this high female density that makes male polygyny possible. At the same time, living at high population density might cause food

shortages if this were initially due to predation pressures rather than enhanced food availability. On the other hand, living in closer proximity may enable group members to exploit their environment more fully through the development of complex social relationships. Thus, coalitions may be at an advantage in interspecific conflict for scarce items so that individuals may actually benefit from a smaller share of a larger total pool. In addition, polygyny tends to promote increased body size in males, because a few extra large individuals can monopolise all the females in a group. It is then conceivable that the presence of these big males not only deters predators, but also reduces interspecific competition, so that females under their protection are able to secure the extra resources that allow them to breed successfully at an earlier age and smaller adult body size. However, these arguments are merely speculative and serve to clarify the problem rather than to offer a definitive solution.

Yet, although facts call for explanations, they do not depend on them and are no less valid because they cannot be accounted for. The present research has found tangible evidence that females of sexually size dimorphic species have been subject to a reduction in adult body size in conjunction with earlier first breeding. This was

shown by allometric analyses of the brain weights and molar tooth areas of simian primates. The results obtained for each of these early maturing components lend credence to the central tenet of the thesis - that most probably for mammals in general and certainly for simian primates in particular, a reduction in adult female body size, in association with earlier first reproduction, has been a key element in the genesis of sexual size dimorphism. An explanation of how and why this should have occurred remains a challenge for future research. The current emphasis is not intended to detract from the significance of increased male body size in promoting sexual size dimorphism. However, early studies frequently ignored the role of selection pressures operating on females and the present findings emphasize the importance of examining the impact of evolutionary forces on both sexes.

7.5 SEXUAL DIMORPHISM IN THE BRAIN

It has been suggested that differences in diet lead to deviations from the allometric relation of brain on body size (Clutton-Brock and Harvey, 1980; Harvey et al., 1987; Milton, 1981). However, this explanation has little relevance to the problem of intersexual differences in adult brain weight within a monomorphic species. These animals are likely to share a common diet as well as the same body size. Why then should there be persistent

differences between the sexes in respect of their absolute brain weights?

A survey of the literature yielded evidence of differences in the organisation of the brain between male and female mammals, but without any corresponding clarification as to their functional significance. However, whereas further investigation of this particular expression of sexual dimorphism is beyond the scope of the present research, the question of intersexual differences in absolute brain size is more immediately accessible. After all, differences in the relative brain weights of males and females, both within and between species, have already been exploited as indicators of evolutionary change in overall body size. It also happens that differences in relative brain weight are automatically translated into somewhat anomalous differences in absolute brain weight when they arise between males and females of monomorphic species. These are conspicuous among the lesser apes and larger New World monkeys, but absent in the smaller species. It is conceivable that they are the residue of a previous dimorphic phase during which time male and female brains were targeted at the respectively different weights commensurate with their different adult body sizes. This interpretation is consistent with the available fossil evidence.

7.6 CONCLUDING REVIEW

It now remains to integrate the present research with existing theories of sexual size dimorphism. These were enumerated in the introduction as: intrasexual selection, intersexual (or epigamic) selection, post-mating sexual selection, niche expansion, anti-predator defence and divergent energy strategies.

7.6.1 Intrasexual selection

In relation to intrasexual selection, the heightened risks experienced by young males of some species, presumably the price of rapid growth at an earlier than usual age, indicate that large body size carries a high premium for these individuals. Perhaps only the fittest and best endowed males survive to compete with each other as sexually mature adults. It is here suggested that the same suite of environmental factors that fostered increased body size in males simultaneously favoured reduced body size in females, with bimaturism arising as a corollary.

7.6.2 Intersexual (or epigamic) selection

Female choice is seemingly manifest in such disparate contexts as the elongated tail of the widow bird and the rejected overtures of sexually, but not yet physically

mature gorillas and orang-utans. Indeed, female preference for older, fully developed males may indirectly protect young males by discouraging them from hazardous attempts to gain access to oestrus females before they have gained the adult stature and characteristics that will make them acceptable as mates.

However, while the consequences of female selection may sometimes be discerned, the underlying motivations often remain enigmatic. Nor is it even consistent in its expression. Clutton-Brock (1985) has cited field studies yielding contradictory evidence for the effects of female preference, noting "that male moorhens are 25% heavier than females, despite female preference for small males". It is always comforting to have a generalised theory of universal application. However, this will not be very durable if it is founded on a restricted sample from the available data and Clutton-Brock powerfully criticises the use of simple illustrations of theoretical arguments that mask "messy facts". Nevertheless, although it may be varied and uneven in the extent of its influence, female choice has probably been a salient evolutionary force in respect of both morphological and behavioural change. This view is endorsed by recent evidence of its occurrence even in monogamous species for which selection in response to female choice might be expected to be weak. Thus, Møller

(1988) has succeeded in showing experimentally that female choice selects for male ornamentation in a monogamous swallow while O'Donald (1987) has made a major contribution by unravelling the frequently confounded effects of intersexual and intrasexual selection. This longitudinal study of arctic skuas gave clear indications of female preference for dark males in comparison with pale individuals. Since fledging success declines as the breeding season proceeds, melanic males gain a reproductive advantage by securing a mate and starting to breed ahead of their competitors. There is evidence that inexperienced males who are breeding for the first time derive the same benefit as older males who have already bred in a previous year - a striking affirmation of the impact of sexual selection in isolation from intrasexual selection.

However, an extensive survey of the literature has yielded no unequivocal evidence linking increased body size among male primates to sexual selection by females. The present research is directed primarily towards the study of sexual size dimorphism rather than that of sexual selection but, since female preference for large males has so often been advanced as an 'explanation' for sexual size dimorphism, its implications cannot be ignored. The view advanced here is that the sophisticated and complex social

organisation characteristic of many species of sexually dimorphic mammals has led sexual selection to be expressed in more subtle and indirect ways than through a unitary increase in adult male body size, although this aspect is not precluded. Thus, a subordinate hamadryas male may be 'courted' by a female so that he develops a bond with her that is subsequently respected by the dominant male (Dunbar, 1986).

Female choice may also be a determinant of male reproductive success among langurs. Manley (1986) has observed that harem males of Presbytis senex are so aggressively defensive that their extreme violence may kill an intruder outright. Female trespassers are not immune to such attacks and may also be harassed and repelled by the older/larger females of the group. Yet females do succeed in initiating themselves into a harem through an elaborate ritual of exchanges with the dominant male. In view of the risks involved, it would seem unlikely that these females have chosen their potential mate on the basis of chance alone.

Krebs and Harvey (1988) have emphasised a common feature of all leks (the aggregation of reproductively active males at a traditional site). Most of the matings are attributable to a very small proportion of the males

on the lek. For example, they cite 90% of matings secured by 3 out of 10 white-bearded manakins, while 5 out of 22 male uganda cobs obtained more than 80% of matings. Such findings not only testify to the importance of female choice, but also raise the question of why and how females distinguish between the competing males. There appears to be a strong correlation between male mating success and display behaviour. If male 'quality' is reflected in the energy available to expend on display, this would nicely resolve both issues. Krebs and Harvey suggest that female choice has "pushed male display behaviour to its physiological limits" and that the most vigorous displayers may also be the most efficient feeders. Mating with such an individual would clearly benefit both the female and her young.

The same authors also remarked that whereas male sage grouse appeared to attract females on the basis of their display behaviour alone, irrespective of the position they occupied on the lek, fallow deer females tended to prefer males occupying specific territories. Since the same sites were consistently preferred in successive years, they were presumably owned by 'high quality' males who had gained them through successful competition. The elaborate structures built by male bower birds are probably yet another example of males advertising the quality of their

genetic endowment. These males must surely invest a great deal of energy in continually refurbishing their edifices and constantly replacing faded flowers. The 'attractiveness' of a structure presumably reflects the effort expended on its maintenance. In contrast, once a female's attention has been engaged, she merely sits passively, intently scrutinising the male's progress, and presumably 'sizing up' his fitness and desirability as a mate (Kevles, 1986).

Despite their diversity, these various examples of sexual selection are all similar in one respect. Females seemingly expend little or no energy in obtaining a mate, whereas an exceedingly high price may be exacted from a male before he is accepted by a female in breeding condition. In some situations, bigger males may be better able to sustain these costs, but this would be a proximate rather than an ultimate factor in promoting intersexual differences in body size. Both sexes seek to mate, but the risks incurred and the energy required to gain this common end are much greater for males than for females. The reproductive effort of a female mammal is concentrated on nurturing her offspring, rather than on securing a mate. Her energy output increases throughout pregnancy and peaks during lactation when she must find the resources to sustain her developing infant, sometimes with direct

paternal assistance, more often without. It would consequently be surprising if males and females had not evolved very different mating strategies and the tenet that sexual size dimorphism is contingent on the divergent energetic needs of males and females accords well with the available data. Meanwhile, the adaptive advantage of sexual selection has been aptly summarised: "natural selection has cloaked the genes of an evolutionarily suitable mate in an attractive package" (Kevles, 1986).

7.6.3 Post-mating sexual selection

As previously intimated (see 1.2.3), post-mating selection is unlikely to have had any bearing on sexual size dimorphism. It does, however, afford an interesting example of strategic female choice. Kevles (1986) reports that among northern elephant seals, Mirounga angustirostris, female preference is initially directed towards the largest, most dominant bulls. Females provoke intense competition between males so that, at least during the earlier part of the breeding season, only the heaviest and strongest animals will have a chance to inseminate them. Subsequently, and just before returning to the sea, these same females court and mate with the younger, smaller males that had previously been ignored and excluded from sexual activity. Le Boeuf et al. (1972) interpret this as a precaution on the part of the female

in case the older, larger bull of her first choice had exhausted his supply of viable sperm prior to copulation. The female ensures that she will be fertilised by electing to mate again, this time with a peripheral young male that can contribute fresh sperm and has not become worn out through the stress of competition and repeated matings.

7.6.4 Niche expansion

The proposition that nich expansion has evoked intersexual differences in adult body size among mammals has already been discounted (1.2.4). The present study has yielded no evidence to modify this assessment.

7.6.5 Divergent energy strategies

It has already been remarked that the degree of sexual sexual size dimorphism can vary considerably, even between closely related species. Explanations have been sought in such factors as diet, ranging behaviour and environmental predictability. However, this style of reasoning is likely to result in a very fragmented approach. Moreover, it would probably be better to regard these aspects as constraints, rather than causes.

Divergent energetic needs are here advanced as the ultimate cause of differences between male and female body sizes, from their inception during development through to adulthood. The extent to which the growth trajectories of

males and females diverge will depend upon intersexual differences in the optimum allocation of the available resources. The nature and quality of the environment will then determine the final expression of sexual size dimorphism between mature individuals.

7.7 SEXUAL SIZE DIMORPHISM IN CONTEXT

The richness of primate culture has allowed the fine tuning of behaviours and social organisation to meet the exigencies of a wide variety of habitats, ranging from tropical rain forests and arid savanna to the freezing winter climate colonised by japanese macaques.

Andelman (1986) examined the ecological and social determinants of cercopithecine mating patterns and, in harmony with the previous discussion, found that there were marked intersexual differences in the energetic costs of reproduction. She reported that female breeding success was usually limited by ecological resources, such as the availability and quality of foods, whereas male reproductive success was limited by the availability of suitable mating partners. Manley's (1986) study of harem accretion in Presbytis entellus led him to a similar conclusion: "It is in the reproductive interests of a male to acquire as many breeding females as can be maintained within a suitable area which he can defend. It is in the

reproductive interests of the female to associate herself with a male who reserves for her and her offspring a food supply and other neccessities of life".

The geneticist Jones (1986) has reported that "experiments on selection in nature suggest that inherited differences in survival are less important than are those associated with mating ability, fertility or fecundity". Yet this would seem to be contradicted by recent evidence for large mammals (R.I.M. Dunbar, pers. comm., Altmann et al., 1985) and for several species of dragonflies and damselflies (Thompson and Dunbar, 1988). The divergence is probably due to differences in the relative importance of key parameters arising in consequence of differences in body size. Since the microscopic Drosophila is the subject of many genetic experiments, the results of these will not necessarily be applicable to other organisms and Thompson and Banks have shown that 70% of the variance in lifetime reproductive output in the damselfly, Coenagrion puella, can be attributed to variation in lifespan for both males and females (Males: Banks and Thompson, 1985; Females: Thompson and Banks, 1987). Thompson and Dunbar also noted the complex relationship that exists between mating success and age among these insects, "older males do much better and younger males do much worse than we might expect", suggesting that as they age, males become

more skilful at locating and capturing females.

Nevertheless, whether fitness depends more on survival or on reproductive output, selection will presumably favour those individuals that have found a solution to the problem of partitioning their resources between growth, maintenance and reproduction that is not only feasible, but approaches an optimum. This universal problem is common to both sexes, but the precise form of the equation will not be the same for males and females. The variables in the equation may be identical, the coefficients will surely differ.

During the course of the present research, both the literature reviewed and the original material contributed have consistently led to the same conclusion - that the life history strategies of male and female mammals are independently dominated by their respective, and different, energetic needs. A tenuous equilibrium must be attained at each successive developmental stage, and males and females will follow sex-specific growth trajectories from birth (or even conception) throughout ontogeny and into adulthood. These may coincide, as they do for monomorphic species, or they may diverge, to an extent that determines the ultimate degree of sexual size dimorphism between mature adults within a species.

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LISTING OF TYPICAL PROGRAM FOR APPENDIX 2.1

```
>L
   10 @%=&20204
   20 INPUT "SIMULATED SAMPLE SIZE",N
   30 INPUT "HOW MANY SIMULATIONS",M
   40 PRINT:PRINT:PRINT:PRINT:PRINT:PRINT:PRINT:PRINT
   70 PRINT
   80 PRINT TAB(10);"SIMULATED SAMPLE SIZE = 50"
   90 PRINT TAB(10);"NUMBER OF SIMULATIONS = 200"
  100 PRINT
  110 GOTO 160
  120 PRINT TAB(6);"CORRELATION",TAB(47);"CORRELATION"
  130 PRINT TAB(5);"COEFFICIENT R",TAB(49);"BETWEEN"
  140 PRINT TAB(6);"(X-Y) : X",TAB(50);"X & Y"
  150 PRINT
  160 LOW=2: HIGH=-2
  170 R1=0: RR1=0: R2=0: RR2=0
  180 FOR K=1 TO M
  190 X1=0: XX1=0
  200 X2=0: XX2=0
  210 Y1=0: YY1=0
  220 Y2=0: YY2=0
  230 Z=0: ZZ=0
  240 FOR I=1 TO N
  250 XX=RND(10):YY=RND(10)
  260 W=ABS(XX-YY)
  270 IF W=0 THEN W=0.1
  280 X=LOG(YY):Y=LOG(W)
  290 X1=X1+X
  300 XX1=XX1+XX
  310 Y1=Y1+Y
  320YY1=YY1+YY
  330 X2=X2+X^2
  340XX2=XX2+XX^2
  350 Y2=Y2+Y^2
  360YY2=YY2+YY^2
  370 Z=Z+X*Y
  380 ZZ=ZZ+XX*YY
  390 NEXT I
  400 R=(Z-X1*Y1/N)/((X2-(X1^2)/N)*(Y2-(Y1^2)/N))^0.5
  410 RR=(ZZ-XX1*YY1/N)/((XX2-(XX1^2)/N)*(YY2-(YY1^2)/N))^0.5
  420 GOTO 490
  430 IF R<0 THEN 460
  440 IF RR<0 THEN PRINT TAB(10);R,TAB(49);RR:GOTO 490
  450 PRINT TAB(10);R,TAB(50);RR:GOTO 490
  460 IF RR<0 THEN PRINT TAB(9);R,TAB(49);RR:GOTO 490
  470 PRINT TAB(9);R,TAB(50);RR:GOTO 490
  480 PRINT TAB(10);R,TAB(50);RR
  490 R1=R1+R: R2=R2+R^2
  500 RR1=RR1+RR: RR2=RR2+RR^2
  510 IF R<LOW THEN LOW=R
  520 IF R>HIGH THEN HIGH=R
  530 NEXT K
  540 PRINT:PRINT
  550 VR=R2/M-(R1/M)^2: VRR=RR2/M-(RR1/M)^2
  560 SER=(VR/M)^0.5: SERR=(VRR/M)^0.5
  570 PRINT TAB(10);"MEAN R(LOG(X-Y):LOG(X)) = ";R1/M,TAB(45)"MEAN R(XY) = ";RR1
/M
  580 PRINT TAB(10);"S.E. R(LOG(X-Y):LOG(X)) = ";SER,TAB(45)"MEAN R(XY) = ":SERR
  590 PRINT:PRINT TAB(11);"                    R(MAX) = ";HIGH
  600 PRINT TAB(11);"                R(MIN) = ";LOW
  610 END
```

CORRELATIONS BETWEEN FUNCTIONS OF X & Y
OBTAINED FROM COMPUTER SIMULATIONS

(See page 302 for program listings)

SIMULATED SAMPLE SIZES: 50
NUMBERS OF SIMULATIONS: 200

MEAN R((X-Y):X) = 0.70
S.E. R((X-Y):X) = 0.00

R(MAX) = 0.83
R(MIN) = 0.50

MEAN R(XY) = 0.02
S.E. R(XY) = 0.01

AS ABOVE WITH VAR(Y) = 2 x VAR(X)

MEAN R((X-Y):X) = 0.83
S.E. R((X-Y):X) = 0.00

R(MAX) = 0.91
R(MIN) = 0.71

MEAN R(XY) = 0.01
S.E. R(XY) = 0.01

MEAN R(LOG(X-Y):LOG(X)) = -0.04

S.E. R(LOG(X-Y):LOG(X)) = 0.01

R(MAX) = 0.41
R(MIN) = -0.41

MEAN R(XY) = 0.01
MEAN R(XY) = 0.01

MEAN R(X/Y:(X+Y)/2) = -0.13
S.E. R(X/Y:(X+Y)/2) = 0.01

R(MAX) = 0.18
R(MIN) = -0.37

MEAN R(XY) = -0.01
S.E. R(XY) = 0.01

DATA SET: BODY AND BRAIN WEIGHTS, AGES AT SEXUAL MATURITY AND LIFESPAN FOR MAMMAL SPECIES

KEY:

WM and WF = Average body weights of males and females in grams

BM and BF = Average brain weights of males and females in milligrams

SM and SF = Average ages at sexual maturity of males and females in months

L(MAX) = Maximum recorded lifespan for species in months

DATA FOR SIMIAN PRIMATES

SPECIES	WM WF	BM BF	SM SF	L(MAX)
ALOUATTA PALLIATA	7343 5824	57150 51480	* 43.2	20.0
AOTUS TRIVIRGARTUS	743 724	17200 17200	* 28.8	20.0
ATELES FUSICEPS	8890 9163	118400 108800	58.8 57.0	*
ATELES GEOFFROYI	7483 7669	112850 104900	* 60.0	27.3
ATELES PANISCUS	9053 8554	106500 101200	* *	*
CALLIMICO GOELDI	582 582	* 11000	16.5 13.9	9.3
CALLITHRIX JACCHUS	289 287	7540 7980	16.7 15.2	11.7
CEBUS ALBIFRONS	2914 2067	65200 60700	* 48.0	44.0
CEBUS APELLA	3281 2201	70800 63500	* 66.0	44.0
CEBUS CAPUCINUS	3432 2578	73400 71890	* 48.0	*
CERCOCEBUS ALBIGENA	8515 6209	113300 94360	* 48.0	32.7
CERCOCEBUS GALERITUS	10183 5473	118500 88850	49.2 *	*

CERCOCEBUS TORQUATUS	115143	116700	*	*
	6333	110500	*	
CERCOPITHECUS AETHIOPS	4878	68400	*	24.0
	3469	60100	42.0	
CERCOPITHECUS ASCANIUS	4273	69300	*	*
	2943	61300	*	
CERCOPITHECUS LHOESTI	8500	93000	*	*
	4700	84500	*	
CERCOPITHECUS MITIS	7374	79500	*	20.0
	4280	56500	51.6	
CERCOPITHECUS MONA	4400	69300	*	*
	2500	62000	*	
CERCOPITHECUS NEGLECTUS	7035	*	72.0	22.0
	4081	*	48.0	
CERCOPITHECUS NICTITANS	6594	75000	*	*
	4216	*	*	
CERCOPITHECUS PYGERYTHRUS	5378	72600	*	*
	3021	65750	*	
COLOBUS BADIUS	8558	*	*	*
	7421	80180	*	
COLOBUS GUEREZA	9797	*	*	*
	7902	72000	*	
COLOBUS POLYKOMUS	10600	*	*	*
	7378	81400	*	
CYNOPITHECUS NIGER	6200	108000	*	18.0
	4600	97500	57.6	
ERYTHROCEBUS PATAS	12600	118000	42.0	21.6
	6317	100000	33.0	
GORILLA GORILLA	143883	530310	120.0	51.0
	85024	457280	78.0	
HYLOBATES AGILIS	5909	92800	*	*
	5530	87600	*	
HYLOBATES LAR	5647	104000	78.0	31.5
	5464	93900	108.0	
HYLOBATES MOLOCH	5967	94900	*	*
	5667	93100	*	
LAGOTHRIX LAGOTRICHA	6670	*	*	25.9
	5540	86200	60.0	

LEONTOPITHECUS ROSALIA	559	*	*	14.2
	559	12300	28.8	
MACACA ARCTOIDES	10050	101600	39.0	*
	8523	99800	26.5	
MACACA FASCICULARIS	5496	71050	*	37.1
	3614	62100	46.8	
MACACA MAURUS	7400	95500	*	*
	*	*	*	
MACACA MULATTA	6368	90000	38.0	29.0
	5445	84700	34.0	
MACACA NEMESTRINA	9951	118300	35.0	*
	5571	110000	*	
MANDRILLUS LEUCOPHAEUS	21400	*	*	*
	8450	124000	*	
MANDRILLUS SPHINX	21530	180000	*	28.6
	11350	*	60.0	
MIOPITHECUS TALOPOIN	1380	*	66.0	*
	1120	37300	48.0	
PAN TROGLODYTES	41970	424500	*	53.0
	34135	380000	134.4	
PAPIO CYNOCEPHALUS	21728	180900	*	*
	11532	164000	*	
PAPIO HAMADRYAS	17960	168300	*	*
	10000	142600	*	
PAPIO PAPIO	19025	193000	*	*
	16166	192000	*	
PAPIO URSINUS	28628	181000	*	*
	14773	164500	*	
PONGO PYGMAEUS	73388	387000	115.0	57.3
	37078	301700	84.0	
PRESBYTIS CRISTATA	6948	75500	*	*
	5856	66000	*	
PRESBYTIS ENTELLUS	15000	119400	*	*
	10280	*	*	
PRESBYTIS OBSCURA	7998	67820	*	*
	6530	60800	*	

PYGATHRIX NEMAEUS	10910	71650	*	*
	8180	*	*	
SAGUINAS GEOFFROYI	473	11800	*	*
	483	10620	*	
SAGUINUS OEDIPUS	408	9250	*	13.5
	425	9650	22.8	
SAIMIRI OERSTEDII	893	*	*	*
	737	25000	*	
SAIMIRI SCIUREUS	805	24700	*	21.0
	699	23000	30.0	
SYMPHALANGUS SYNDDACTYLIS	11086	132600	*	35.0
	10568	130000	108.0	
TARSIUS SYRICHTA	129.5	*	*	*
	120.5	3300	*	
THEROPITHECUS GELADA	19420	121000	*	19.3
	11700	119700	48.0	

DATA FOR PROSIMIAN PRIMATES

AVAHI LANIGER	853	9667	*	*
	875	10560	*	
CHEIROGALEUS MEDIUS	185	3090	*	*
	*	*	*	
DAUBENTONIA MADAGASCARENSIS	*	*	*	*
	2800	44050	*	
GALAGO CRASSICAUDATUS	1355	10650	*	*
	1170	9770	*	
GALAGO DEMIDOVII	66.7	3340	*	9.0
	62.8	3340	12.0	
GALAGO SENEGALENSIS	*	*	*	16.5
	179	5000	10.8	
INDRI INDRI	*	*	*	*
	6250	38300	*	
LEMUR CATTA	*	*	*	27.1
	2290	22600	24.0	
LEMUR FULVUS	1973	23300	*	30.1
	*	*	27.6	

LEMUR MACACO	2428	23600	*	*
	*	*	*	
LEMUR MONGOZ	*	*	*	*
	1890	23800	*	
LEPILEMUR RUFICAUDATUS	803	6900	*	*
	803	7790	*	
LORIS TARDIGRADUS	277	6100	*	12.0
	*	*	18.0	
PERODICTUS POTTO	972	13900	*	22.3
	935	13500	24.0	
PROPITHECUS VERREAUXI	3585	26700	*	18.2
	3183	26700	33.6	
VARECIA VARIEGATA	3500	32000	*	13.0
	2700	31000	20.4	

DATA FOR NONPRIMATE MAMMALS

ARTIODACTYLA: BOVIDAE

ACEPHALUS BUSELAPHUS	168200	275000	12.0	20.3
	169300	*	24.0	
AEPYCEROS MELAMPUS	60000	*	13.0	12.7
	45000	*	24.5	
AYRSHIRE CATTLE	*	*	*	*
	491000	417000	*	
BUBLIS COKEI	134000	275000	*	*
	*	*	*	
CAPRA HIRCUS	27600	110500	*	*
	*	*	*	
CEPHALOPHUS MONTICOLOR	6250	*	36.0	10.0
	6250	*	36.0	
CEPHALOPHUS SYLVICULTOR	625000	*	*	9.0
	625000	*	*	
CONNOCHAETES TAURINUS	200000	*	60.0	24.0
	160000	*	32.0	19.0
DAMALISCUS LUNATUS	142000	*	20.0	*
	130000	*	36.0	
FLORIDA CATTLE	369000	384000	*	*
	*	*	*	

GAZELLA THOMSONII	22500	91800	24.0	10.9
	18500		18.0	
GUERNSEY CATTLE	*	*	*	*
	450000	403000	*	
HEREFORD CATTLE	*	*	*	*
	371000	357000	*	
HIPPOTRAGUS EQUINUS	280000	*	*	*
	260000	*	24.0	
HIPPOTRAGUS NIGER	235000	*	19.6	16.7
	220000	*	19.6	
HOLSTEIN CATTLE	888000	462000	10.9	*
	574000	415000	11.3	
JERSEY CATTLE	412000	408000	*	*
	413000	408000	*	
MADOQUA KIRKII	5100	37000	9	*
	5500	*	15.6	
NEOTRAGUS MOSCHATUS	6500	*	14.0	*
	6500	*	12.0	
OREOTRAGUS OREOTRAGUS	12500	*	12.0	*
	12500	*	*	
OUREBIA OUREBI	16500	*	14.0	14.0
	18000	*	10.0	
RAPHICEROS CAMPESTRIS	12370	49500	7.5	*
	11790	*	12.0	
REDUNCA ARUNDINUM	68000	*	36.0	*
	48000	*		
REDUNCA REDUNCA	49100	109000	*	10.0
	40500	*	*	
RHYNCHOTRAGUS KIRKI	4570	37000	6.0	9.5
	5500	*	6.0	
SYLVICAPRA GRIMMIA	18500	*	*	12.0
	20500	*	12.0	
SYNCERUS CAFFER	759000	665000	36.0	26.0
	480000	*	48.0	
TAUROTRAGUS ORYX	690000	*	48.0	25.0
	450000	*	36.0	
TRAGELAPHUS SCRIPTUS	71490	190000	30	12.0
	47400	140000		

TRAGELAPHUS SPEKEI	102000	*	48	20.0
	53500	*		
TRAGELAPHUS STREPICEROS	257000	*	14.0	15.0
	170000	*	14.0	
ARTIODACTYLA: CAPRINAE				
CAPRA HIRCUS	27600	115000	*	18.0
	*	*	*	
ARTIODACTYLA: CERVIDAE				
CERVUS AXIS	88450	219000	*	*
	*	*	*	
CERVUS CANADENSIS	13610	194200	*	*
	*	*	*	
DAMA DAMA	39000	*	16.0	*
	39000	*		
MOSCHUS MOSCHIFERUS	10000	*	12.0	*
	10000	*	12.0	
ODOCOILEUS HEMIONUS	*	123000	*	*
	57000	*	*	
ODOCOILEUS VIRGINIANUS	65090	210000	*	*
	13930	*	*	
RANGIFER ARCTICUS	128470	306000	*	*
	71700	278000	*	
RANGIFER TARANDUS	106360	299000	15.0	15.0
	105000	278000		
ARTIODACTYLA: GIRAFFIDAE				
GIRAFFA	1100000	700000	84.0	28.0
CAMELOPARDALIS	700000	*	63.0	
ARTIODACTYLA: HIPPOPOTAMIDAE				
CHOEROPSIS	272000	*	51.0	40.0
LIBERIENSIS	272000	*	51.0	
HIPPOPOTAMUS	1475000	*	90.0	50.0
AMPHIBIUS	1360000	720000	108.0	
ARTIODACTYLA: SUIDAE				
PHACOCHOERUS	88200	125000	*	*
AETHIOPICUS	61700	*	*	

SUS SCROFA	75000	*	18.0	*
	75000	*	18.0	
ARTIODACTYLA: TRAGULIDAE				
TRAGULUS JAVANICUS	1500	*	4.5	*
	1500	*	4.5	
CETACEA				
BALAENOPTERA	81826000	*	51.0	*
MUSCULUS	116087000	*	51.0	
BALAENOPTERA	42190000	*	51.0	*
PHYSALIS	52337000	*	51.0	
DELPHINAPTERUS	441310	2349000	*	*
LEUCUS	303230	2354000	*	
LAGENORHYNCUS	93333	1156000	*	*
OBLIQUIDENS	79000	1079000	*	
PHOCAENA PHOCAENA	142430	1735000	*	*
	*	*	*	
PHOCOENOIDES DALLI	*	*	*	*
	98000	834000	*	
TURSIOPS TRUNCATUS	75000	1438000	*	*
	91000	1384000	*	
EDENTATA				
CHOLOEPUS HOFFMAN1	*	*	*	11.0
	5272	26000	*	
DASYPUS NOVEMCINCTUS	2086	9500	*	*
	*	*	*	
FISSIPEDIA: CANIDAE				
CANIS FAMILIARIS	14560	79990	*	*
	12470	81140	*	
CANIS LATRANS	*	*	*	15.0
	8510	82120	*	
CANIS LUBILUS	29940	152000	*	*
	*	*	*	
CANIS LUPUS	26310	135500	*	14.0
	*	*	*	
CANIS MESOMELES	2850	46000	*	14.0
	*	*	*	

OTOCYON MEGALOTIS	*	*	*	*
	3335	26090	*	
THOS MESOMELAS	2850	46000	*	*
	*	*	*	
UROCYON CINEREO	3749	37280	*	8.4
	*	*	*	
VULPES FULVA	*	*	*	12.0
	4625	53300	*	
VULPES LAGOPUS	3385	44500	*	*
	*	*	*	
VULPES VULPES	6700	*	10.0	9.75
	5400	*	10.0	
<u>FISSIPEDIA: FELIDAE</u>				
ACINONYX JUBATUS	55000	*	15.0	15.6
	45000	*	21.5	
FELIS BANGSI	25960	129000	*	*
	*	*	*	
FELIS CACOMISTLI	*	*	*	*
	2722	41900	*	
FELIS CAPENSIS	9955	66740	*	*
	5819	53160	*	
FELIS CARACAL	16750	*	15.0	17.0
	15250	*	15.0	
FELIS CONCOLOR	28790	106700	*	*
	*	*	*	
FELIS DOMESTICUS	3778	28370	*	*
	2885	23460	*	
FELIS LEO	172000	258000	48.0	30.0
	151000	*	*	
FELIS NIGRIPES	1620	*	21.0	*
	1620	*	21.0	
FELIS OCREATA	*	*	*	*
	2700	28480	*	
FELIS ONCA	*	*	*	*
	34470	147000	*	
FELIS OREGONENSIS	28790	106700	*	*
	*	*	*	

FELIS PARDALIS	9525	63100	*	*
	*	*	*	
FELIS SERVAL	13000	54100	*	13.0
	11000	*	*	
FELIS SYLVESTRIS	5000	*	15.0	21.0
	4300	*	*	
FELIS TIGRIS	209000	302000	*	*
	160000	225000	*	
LYNX CANADENSIS	14969	69500		11.6
	*	*		
LYNX RUFELIDAEUS	6350	65000	*	*
	*	*	*	
PANTHERA TIGRIS	13400	*	54.0	19.5
	13400	*	54.0	
FISSIPEDIA: MUSTELIDAE				
MELES MELES	11600	*	24.0	14.0
	10100	*	13.0	
MEPHITIS MEPHITIS	1700	10300	*	10.0
	2260	10000	*	
MUSTELA ARCTICA	169	5640	*	*
	121	3470	*	
MUSTELA VISON	793	*	12.0	10.0
	793	*	12.0	
PUTORIUS PUTOR	915	7870	*	*
	*	*	*	
FISSIPEDIA: PROCYONIDAE				
AILURUS FULGENS	3750	*	18.7	*
	3750	*	18.7	
NASUA NARICA	6250	44170	*	11.0
	*	*	*	
POTOS CAUDIVARUS	1863	35100	*	*
			*	
POTOS FLAVUS	*	*	*	19.4
	2620	31050	*	
PROCYON LOTOR	5216	42700	18.0	13.8
	3380	37000	18.0	
FISSIPEDIA: URSIDAE				

HELARCTOR MALAY	*	*	*	20.5
	45020	385000	*	
MELURSUS URS	*	*	*	*
	136080	267000	*	
URSUS MARITIMUS	199570	489000	*	33.3
	317000	507000	*	
URSUS HORRIBILIS	149688	389000	*	*
	142880	233900	*	
FISSIPEDIA: VIVERRIDAE				
CROCUTA CROCUTA	48700	*	24.0	25.0
	55300	*	36.0	
GENETTA TIGRINA	- 1302	15890	*	*
	1525	15350	*	
ICHNEUMIA ALBICAUDA	4400	28300	*	*
	*	*	*	
HOMINOIDEA: HOMINIDAE				
HOMO SAPIENS	64800	*	174.0	104.0
	60000	*	162.0	
HYRACOIDEA: PROCAVIIDAE				
HETEROHYRAX BRUCEI	750	12270	*	*
	*	*	*	
PROCAVAI CAPENSIS	17000	*	24.0	6.2
	17000	*	24.0	
INSECTIVORA: MACROSCELIDIDAE				
ELEPHANTULUS FUSICEPS	52	1290	*	*
	62	1360	*	
RHYNCHOCYON STUHLMANNI	474	6200	*	*
	502	6000	*	
INSECTIVORA: SORICIDAE				
BLARINA BREVICAUDATA	20	350	*	*
	17	360	*	
CROCIDURA GIFFARDI	82	550	*	*
	*	*	*	
CROCIDURA HILDEGARDAE	11.6	220	*	*
	9.7	200	*	

CROCIDURA NIOBE	9.5	280	*	*
	*	*	*	
CROCIDURA OCCIDENTALIS	32	450	*	*
	24	430	*	
CROCIDURA RUSSULA	10.6	180	*	*
	*	*	*	
SOREX ARANEUS	9.5	190	9.2	*
	8.5	200	9.2	
SOREX MINUTUS	4.85	110	*	*
	5.30	110	*	
SUNCUS MURINUS	43.8	390	*	*
	27.2	370	*	
INSECTIVORA: TALPIDAE				
CHLOROTALPA STUHLMANNI	46.0	780	*	*
	34.5	690	*	
GALEMYS PYRENAICUS	63.2	*	*	*
	51.8	*	*	
SCALOPUS AQUATICUS	39.6	*	*	*
	*	*	*	
TALPA EUROPEA	84	1030	5.9	*
	68	1010	5.9	
INSECTIVORA: TENRECIDAE				
ECHINOPS TELFAIRI	72	580	6.0	*
	102	670	6.0	
HEMICENTETES SEMISPINOSUS	76.6	740	*	1.8
	114.1	830	1.2	
SETIFER SETOSUS	218.8	1590	6.0	*
	256.3	1450	6.0	
TENREC ECAUDATUS	2000	*	6.0	2.3
	900	*	6.0	
PERISSODACTYLA				
EQUUS ASINUS	211000	371000	*	*
	291000	478000	*	
EQUUS BURCHELLI	318500	*	27.0	27.8
	321600	*	27.0	
EQUUS CABALLUS	485310	706700	*	50.0
	443360	637700	*	

EQUUS QUAGGAI	317500	642000	*	*
	*	*	*	
RHINOCERUS BICORNIS	763000	655000	*	*
	*	*	*	
PINNIPEDIA				
ODOBENUS ROSMARUS	667000	1126000	84.0	15.0
	560000	*	54.0	
CALLORHINUS URSINUS	*	*	36.0	25.0
	55000	*	36.0	
CRYSTOPHORA CRISTATA	*	*	48.0	*
	270000	*	48.0	
ERIGNATHUS BARBATUS	*	*	84.0	*
	281000	460000	72.0	
HALICHOERUS GRYPUS	131818	*	96.0	25.0
	95455	*	54.0	35.0
MIROUNGA LIONINA	900000	*	48.0	*
	420000	*	24.0	
PAGOPHILES GROENLANDICUS	*	*	96.0	*
	140000	*	78.0	
PHOCA HISPIDA	39460	251000	*	*
	39680	255000	*	
PHOCA RICHARDI	107300	442000	*	*
	*	*	*	
PROBOSCIDEA: ELEPHANTIDAE				
LOXODONT AFRICANA	6654000	5712000	168	45.3
	2800000	*	192	
RODENTIA				
CASTOR CANADENSIS	4180	25480	30.0	9.0
	5830	29520	30.0	
CAVIA CUTLERI	456	4230	*	*
	432	4000	*	
CHINCHILLA LANIGER	500	*	6.4	*
	500	*	6.4	
CITELLUS PARYII	878	5630	*	*
	958	5740	*	

CRICETUS CRICETUS	200	*	1.4	2.5
	200	*	1.4	
CUNICULUS PACA	4559	48000	*	*
	*	*	*	
DICROSTONYX RUBRICATUS	52.1	898	*	*
	*	*	*	
ERINACEUS EUROPAEUS	895	3400	*	*
	842	3460	*	
GLAUCOMYS VOLANS	60	*	12.0	6.0
	60	*	12.0	
LEMMUS TRINUCRONATUS	48	1312	*	*
	32	1126	*	
LEPUS ARCTICUS	2640	13900	*	*
	1901	14360	*	
LEPUS CAPENSIS	*	*	*	*
	2930	10230	*	
LEPUS FLEMISH	3680	10590	*	*
	2587	10140	*	
MARMOTA MONAX	5500	*	24.0	*
	5500	*	24.0	
MESOCRICATUS AURATUS	90	*	2.1	*
	90	*	2.1	
MICROTUS PENNSYLVANICUS	27.9	739	*	1.3
	*	*	*	
MUS NORVEGICUS	278	2300	*	*
	197	1610	*	
MYSTROMIS ALBICAUDATUS	122	*	1.1	*
	122	*	1.1	
NESOGALI DOBSONI	34	560	*	*
	*	*	*	
NESOGALI TALAZACI	40.6	750	*	*
	45	780	*	
ONDATRA ZIBETHICA	900	5330	*	*
	*	*	*	
PERROMYSCUS GOSSIPINUS	29	*	0.8	*
	29	*	0.8	

SCIURUS HUDSONICUS	183	4710	*	*
	248	5020	*	
TAMIASCURUS	190	*	14.0	8.0
HUDSONICUS	190	*	14.0	
TUPAIA BELANGERI	200	*	3.0	*
	200	*	3.0	
TUPAIA GLIS	143	3130	*	*
	157	3140	*	
TUPAIA JAVANICA	102	2550	*	8.0
	*	*	*	
UROGALE EVERETTI	275	4280	*	*
	*	*	*	

APPENDIX 2.3

MATERNAL AND NEONATAL BODY WEIGHTS, GESTATION PERIOD AND AVERAGE LITTER SIZE FOR SIMIAN PRIMATES

KEY:

WM = Average body weight of females in grams
WN = Average body weight of neonate in grams
G = Gestation period in days
L = Average litter size

SPECIES	WM	WN	G	L
Alouatta palliata	5824	480	186	1.1
Aotus trivirgartus	724	97	186	1.0
Ateles geoffroyi	7669	426	225	1.0
Callimico goeldi	582	50.6	155	1.0
Callithrix jacchus	287	27	148	2.0
Cebuella pygmaea	79	15	137	2.0
Cebus albifrons	2067	234	155	1.0
Cebus apella	2201	239.7	155	1.0
Cercocebus albigena	6209	425	176	1.0
Cercopithecus aethiops	3469	314	163.3	1.0
Cynopithecus niger	4600	455	170.9	1.0
Erythrocebus patas	6317	504.5	167.5	1.0
Gorilla gorilla	85024	2122.9	259	1.0
Hylobates lar	5464	400	213	1.0
Lagothrix lagotricha	5540	450	223	1.0
Leontopithecus rosalia	559	50	128	2.0
Macaca arctoides	8523	485	178	1.0
Macaca fascicularis	3614	346	160	1.0
Macaca fuscata	9100	496	173	1.0
Macaca mulatta	5445	488	164	1.0
Macaca nemestrina	5571	472	167	1.0
Mandrillus sphinx	11350	613	174.6	1.0
Pan troglodytes	34135	1742	234.5	1.0
Papio cynocephalus	11532	854	172.6	1.0
Pongo pygmaeus	37078	1735	270	1.0
Saguinus oedipus	425	44	168	1.0
Saimiri sciureus	699	95.2	170.5	1.0
Symphalangus syndactilis	10568	517	232	1.0
Theropithecus gelada	11700	553	170	1.0

WEIGHTS AND DENTAL MEASUREMENTS OF SIMIAN PRIMATES

KEY:

BW = Average body weight in grams
M_1 L = Average length of lower first molar tooth (mm)
M_1 W = Average width of lower first molar tooth (mm)

SPECIES		BW	M_1 L	M_1 W
Aotus trivirgatus	(m)	743	3.3	4.1
	(f)	724	3.3	3.9
Alouatta seniculus	(m)	7340	7.47	7.99
	(f)	5807	7.1	7.3
Alouatta villosa	(m)	7400	7.1	8.1
	(f)	5700	6.9	7.3
Ateles geoffroyi	(m)	7483	4.9	5.5
	(f)	7669	5.3	5.7
Cebus apella		3281	4.69	6.31
	(f)	2201	4.56	6.04
Cercocebus albigena	(m)	8515	7.0	6.73
	(f)	6209	6.56	6.22
Cercocebus galeritus	(m)	10183	7.3	8.1
	(f)	5473	7.1	7.4
Cercocebus torquatus	(m)	11514	7.5	7.8
	(f)	6366	7.2	7.6
Cercopithecus aethiops	(m)	4878	5.74	5.59
	(f)	3469	5.36	5.23
Cercopithecus ascanius	(m)	4273	5.09	4.78
	(f)	2943	4.91	4.76
Cercopithecus cephus	(m)	4100	5.7	5.3
	(f)	2900	5.4	5.1
Cercopithecus mitis	(m)	7374	6.1	5.5
	(f)	4280	5.9	5.4
Cercopithecus mona	(m)	4400	5.3	5.2
	(f)	2500	5.3	5.0
Cercopithecus neglectus	(m)	7035	6.3	5.5
	(f)	4081	5.9	5.2
Cercopithecus nictitans		6594	5.6	5.1
	(f)	4216	5.5	5.1

continued....

APPENDIX 2.4 (continued)

SPECIES		BW	M_1 L	M_1 W
Colobus badius	(m)	8558	7.0	6.0
	(f)	7421	6.9	6.0
Colobus polykomos	(m)	10600	7.0	6.5
	(f)	7378	6.8	6.2
Cynopithecus niger	(m)	6200	7.1	6.5
	(f)	4600	6.4	6.0
Gorilla gorilla	(m)	143883	15.7	15.4
	(f)	85024	14.8	15.0
Hylobates klossi		5900	5.5	5.9
	(f)	5700	5.2	5.7
Hylobates agilis	(m)	5909	5.7	6.0
	(f)	5530	5.6	6.0
Hylobates moloch	(m)	6000	5.9	6.5
	(f)	5700	5.7	6.3
Macaca fascicularis	(m)	5496	6.5	6.4
	(f)	3614	6.3	6.2
Macaca mulatta	(m)	6368	7.2	7.0
	(f)	5445	7.1	6.8
Macaca nemestrina	(m)	9951	7.4	7.2
	(f)	5571	7.1	7.1
Nasalis larvatus	(m)	20564	7.0	6.3
	(f)	9550	6.8	6.0
Pan troglodytes	(m)	41970	10.3	11.7
	(f)	34135	10.1	10.9
Pongo pygmaeus	(m)	73388	12.8	13.8
	(f)	37078	11.9	12.2
Presbytis cristata	(m)	6948	5.95	5.88
	(f)	5856	5.79	5.84
Saguinas geoffroyi	(m)	473	2.8	3.6
	(f)	483	2.9	3.9
Saimiri oerstedii	(m)	893	2.8	3.9
	(f)	737	2.7	3.7
Saimiri sciureus	(m)	805	2.8	4.1
	(f)	699	2.8	4.0

WEIGHTS AND DENTAL MEASUREMENTS OF MUSEUM SPECIMENS

KEY:

BW = Body weight in grams
M_1 L = Length of lower first molar tooth
M_1 W = Width of lower first molar tooth
N = Museum specimen number

Presbytis obscura

N	M_1 L	M_1 W	BW	Sex
71.733	6.55	4.90	9060	M
71.734	6.20	5.10	6795	M
71.722	6.45	4.85	8154	M
71.718	6.30	4.75	7475	M
71.728	6.15	4.60	7248	M
71.735	6.20	4.99	7701	M
71.729	5.95	4.99	7701	M
71.709	6.45	4.75	7248	M
71.711	5.70	4.45	5889	F
71.707	6.20	5.35	6795	F
71.724	5.30	4.65	6342	F
71.708	6.05	5.20	pregnant	F
71.710	5.50	4.70	6342	F
71.720	5.70	4.75	7928	F
71.721	6.20	5.05	7928	F
71.703	6.35	4.99	6339	F
71.705	5.80	4.95	6790	F
71.736	6.25	5.00	7022	F
71.737	5.50	5.10	6790	F
71.704	6.30			

Cercopithecus mitis

72.76	6.55	4.90	8955	M
72.68	6.50	4.85	7375	M
72.72	6.10	4.60	7054	M
72.90	6.20	4.60	7930	M
72.53	5.50	4.85	7640	M
72.52	5.70	4.60	6515	M
72.78	5.50	4.25	5170	F
72.71	6.55	5.15	4160	F
72.63	6.25	4.95	5140	F
72.58	6.25	4.50	3960	F
72.62	6.30	4.50	3640	F
72.54	5.65	4.05	3448	F